Drivers, dynamics and management of Eastern Baltic cod (*Gadus morhua*) reproduction habitat

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Content

Summary

The overall increasing hypoxic conditions within the Eastern Baltic cod reproduction habitat are induced by anthropogenic eutrophication and have adverse consequences for the cod population. A continuously high fishing pressure contributes also to the mechanisms that retain the stock at low levels and is shifting its size structure towards small individuals further hampering the reproductive success. Therefore, the overall aim of my thesis was to improve our understanding of environmental drivers causing this development and the dynamics of the Eastern Baltic cod reproduction habitat and to assess their relevance for a possible application in the sustainable stock management. The advanced process knowledge of the hydrographic system of the Baltic Sea and the female spawner size depending differences in egg buoyancy were used to quantify and qualify the environmental spawning habitat. Additionally, a particle tracking technique to simulate the passive drift of egg and larval was used to examine the potential availability and occupation of nursery habitats in light of the expanding hypoxic zones.

A novel approach to map the reproductive habitat of Eastern Baltic cod, the Buoyancy Depending Reproductive Layers (BDRL), was developed and used to propose an alternative stock indicator, the effective Spawning Stock Biomass (eSSB). The eSSB combined female size dependent depths of neutral egg buoyancy with a model of oxygen depending egg survival to exclude those females from the potential reproductive stock, which produce eggs not buoyant enough to escape the low oxygen conditions within the deeper water layers. The eSSB was found to improve the fit of a Ricker-Type recruitment model compared to the model using the conventional Spawning Stock Biomass (SSB not considering any abiotic environmental conditions). Therefore, the stock size structure has strong relevance to fishing efforts, due to the relevance for the stock recruitment and the proposed eSSB should be considered to be applied supporting the efforts to give scientific advice on sustainable catches.

Oxygen depletion was also negatively impacting the available size of nursery areas for juveniles. The proportional usage of adjacent nursery habitats was further heavily influenced by drift off of eggs and larvae from the spawning grounds. When combined, these mechanisms were able to partly explain the observed decline of the condition of juveniles in the nursery areas, because a high population density in the remaining habitat could increase the impact of density depending effects (such as food competition). The most important spawning ground in the current situation of low nursery areas availability, identified by the proportional possible contribution to the amount of successfully settled juveniles, was found to be the Bornholm Basin.

Furthermore, by the application of the novel approach of BDRLs the spawning habitat was shown to be sensitive to eutrophication and that this sensitivity is strongly depending on the size of the female spawner using the habitat. A reduction of eutrophication by 30% significantly improved the environmental spawning conditions especially for small Eastern Baltic cod individuals. As predicted, the BDRL approach was superior to the “classic” approach, the Reproductive Volume (RV) because it was more sensitive to environmental change, able to incorporate stock structure, was not overestimating the spawning habitat in the eastern spawning areas (Gdansk Deep and Gotland Basin) and could provide estimates of other stressors or derived indicators depending on the female spawner size.

Due to the advanced hydrographic process knowledge and a permanently installed measurement platform for abiotic data in the Arkona Basin, the new methodology could be used to establish a new environmental indicator on the spawning habitat conditions each year. This indicator was able to produce short term forecasts for the survival of eggs in the Bornholm Basin spawned by the most abundant size classes of the stock and was recommended to be used in future stock assessments to incorporate an environmental factor in the recruitment estimates.

Overall the results indicated that the reproduction habitat of Eastern Baltic cod is currently in a low quality state and that recruitment processes of the stock are partly stock size structure dependent. The proposed approach of individualized BDRLs was shown to be ready and sufficiently developed to be used in future studies on the impact of environmental change on the spawning habitat of Eastern Baltic cod (e.g. eutrophication, ocean acidification, climate change). Furthermore, the BDRL approach should be utilized to inform the yearly stock assessment on egg survival chances ahead of time improving recruitment estimates and sustainable stock management.

Zusammenfassung

In der Ostsee hat der sich verstärkende Sauerstoffmangel im Reproduktionshabitat des Dorsches anthropogenen Ursprung und ist einer der wichtigsten Gründe warum die Population momentan unter einer schlechten Entwicklung leidet. Zusätzlich sorgt auch ein zu hoher Fischereidruck für einen geringen Bestand und verändert die Längenstruktur zunehmend so, dass sie im Moment von sehr kleinen Individuen dominiert wird. Das Ziel dieser Arbeit war deshalb unser Verständnis der treibenden Umweltparameter dieser Entwicklung und ihrer Dynamic zu verbessern und sie auf eine mögliche Nutzung im Zusammenhang mit einem nachhaltigen Management des Bestandes zu überprüfen. Zur Quantifizierung und Abschätzung der abiotischen Qualität des Laichhabitats wurden die fortgeschrittenen Kenntnisse des hydrographischen Systems der Ostsee als auch die vorhandenen Unterschiede in der Schwebfähigkeit der Eier von unterschiedlich großen Weibchen genutzt. Zusätzlich wurde noch eine Modellierungstechnik zur Verfolgung von passiv driftenden Partikeln eingesetzt, um die Größe und die relative Nutzung von Jungfischhabitat auf dem Hintergrund der zunehmenden sauerstoffarmen Zonen zu untersuchen.

Entwickelt wurde eine neue Methode die das Laichhabitat des Ostseedorsches mit der Hilfe von Dichteflächen kartiert, die dem Auftrieb von Dorscheiern entsprechen (the Buoyancy Depending Reproductive Layer approach, BDRL). Die neu entwickelte BDRL-Methode wurde genutzt, um einen alternativen Bestandsindikator vorzuschlagen: die effektive Laicherbestandsbiomasse (eSSB, effective Spawning Stock Biomass). Der eSSB kombiniert die Relation zwischen Eischwebfähigkeit und Rognergröße mit dem sauerstoffabhängigen Überleben der Eier, da die Schwebfähigkeit entschiedet ob die Eier den niedrigen Sauerstoffverhältnissen in den tiefen Schichten der Becken ausgesetzt sind. So konnten Weibchen mit sehr geringen Fortpflanzungschancen in den jeweiligen Jahren aus dem Laicherbestand herausgenommen werden und so der herkömmliche SSB in den effektiven SSB umgewandelt werden. Es konnte nachgewiesen werden, dass der eSSB die Anpassung eines Rekrutierungsmodells des Ricker-Typs gegenüber dem konventionellen SSB, der keine Umweltparameter einfließen lässt, verbessert. Die Längenstruktur des Bestandes hat damit starken Einfluss auf den Rekrutierungsprozess und damit auch Relevanz für die nachhaltige Befischung des Bestandes und sollte auch in der Findung der wissenschaftlichen Empfehlung zu nachhaltigen Fängen eine Rolle spielen.

Desweitern wurde in dieser Arbeit nachgewiesen, dass die Sauerstoffarmut in der Ostsee auch die Jungfischhabitate des Ostseedorsches negativ beeinflusst. Die proportionale Nutzung der an die Laichgebiete angerenzenden Jungfischhabitate wurde zusätzlich stark davon beeinflusst, dass Individuen während der Ei und Larvenphase mit den Wasserströmungen verdriftet wurden. Zusammengenommen könnten diese beiden Mechanismen den starken Rückgang in der Kondition der Jungfische teilweise erklären, da das limitierte Habitat und die überproportionale Nutzung einzelner Gebiete zu negativen Effekten führen könnten, die durch eine erhöhte Dichte von Individuen im Habitat verursacht werden (z.B. Nahrungskonkurrenz). Auf diesem Hintergrund wurde das Laichgebiet mit den größten Erfolgschancen für die dort gelegten Eier sich nach der Larvenphase erfolgreich als Jungfisch in geeignetem Habitat niederzulassen als das Bornholm Becken identifiziert.

Durch die Nutzung der neu entwickelten BDRL-Methode wurde weiterhin festgestellt, dass das Laichhabitat sensitiv gegenüber Änderungen des Eutrophierungsgrades der Ostsee

reagiert und das diese Reaktion unterschiedlich stark ausfällt, abhängig von der Größe des Rogners. Eine Reduktion der Eutrophierung um 30% würde insbesondere die Umweltbedingungen zum Laichen von kleinen Rognern signifikant positiv beeinflussen. Im Vergleich mit dem herkömmlichen Ansatz zur Einschätzung der Umweltbedingungen im Laichhabitat des Ostseedorsches, der Berechnung des Reproduktionsvolumens (RV), ist die Methode der BDRLs als überlegen anzusehen: Sie reagiert sensibler gegenüber Änderungen in den Umweltbedingungen, kann die Demographische Struktur des Bestandes berücksichtigen, überschätzt nicht die Größe des geeigneten Habitats in den östlichen Laichgebieten (Danziger Tief und Gotland Becken) und ist in der Lage Stressfaktoren oder Umweltindikatoren abzuschätzen, die die Rognergröße berücksichtigen.

Durch ein fortgeschrittenes Verständnis des hydrographischen Systems und der Nutzung vorhandener und betriebsbereiter Überwachungstechnik, eine dauerhaft installierte Messplattform für abiotische Umweltparameter im Arkona Becken, konnte die neue BDRL-Methode außerdem für die Entwicklung eines neuen Umweltindikators, der die Bedingungen im Laichhabitat jedes Jahr abschätzt, herangezogen werden. Dieser Indikator ist in der Lage kurzfristige Voraussagen über das Überleben von Eiern der dominierenden Längenklassen im Bestand im Bornholm Becken zu treffen und wird in dieser Arbeit deshalb dafür empfohlen in den routinemäßigen Bestandsanalysen als Umweltfaktor in den Rekrutierungsmodellen genutzt zu werden.

Im Ganzen betrachtet zeigen die Resultate dieser Arbeit, dass das Reproduktionshabitat des Ostseedorsches in einem Zustand schlechter Qualität verweilt und dass Rekrutierungsprozesse im Bestand auch von der Längenstruktur des Bestandes abhängen. Außerdem konnte gezeigt werden, dass die vorgeschlagene BDRL-Methode bestandsrelevante Prozesse abbildet und weit genug entwickelt ist, um für kommende Studien von Umweltentwicklungen, die das Reproduktionshabitat beeinflussen, wie z.B. Eutrophierung, Ozeanversauerung oder Klimawandel, eingesetzt zu werden. Sie sollte außerdem dafür genutzt werden, um die Rekrutierungsabschätzung in der jährlichen Bestandsanalyse zu verbessern.

Introduction

For all marine species, salinity and oxygen are of paramount importance, governing physiological processes essential for survival. Teleost fish occupy a large range of habitats from freshwater systems to highly saline environments. Sub populations of Atlantic cod (*Gadus morhua*) can be found from oceanic waters (S = 35) to the brackish water of the eastern Baltic Sea (S = 5-6). Reproductive strategies and mechanisms are partly adapted to these environments, e.g. by differences in osmoregulation and oocytes development (Berg et al., 2015). The Eastern Baltic cod population is living at the species' physiological limit making it vulnerable to environmental changes (Köster, 2016). During the last 20 years due to climate change and anthropogenic eutrophication, oxygen minimum zones in marine systems expanded worldwide (Stramma et al., 2010), with adverse consequences for marine life especially in coastal environments (Diaz et al., 2008). These "dead zones" are expected to further expand in the future (Oschlies et al., 2009). The overall impact of climate change on fisheries worldwide is controversially debated (Pinnegar et al., 2013), however, for the Baltic Sea climate scenarios need to be considered for sustainable fisheries management, because oxygen depletion has already a negative impact on the recruitment processes (Lindgren et al., 2010).

For all species, habitat conditions in the Baltic Sea are mainly driven by the salinity gradient and stratification (Zettler et al., 2014; Ojaveer et al., 2010; Herlemann et al., 2011), which in turn is depending on the oceanographic mechanisms driven by atmospheric forcing. The Baltic Sea is unique in regard to how these mechanisms influence oxygen related processes, causing the recent increase of hypoxic zones to be accelerated compared to other coastal environments in the world (Conley et al., 2009, 2011). Hence, using the Baltic Sea and its resident fish populations as an example, gives us the opportunity to understand the future development in other seas (Reusch et al., 2018) since we can study already now how oxygen depletion impacts species habitats and develop viable tools for integrated ecosystem based management.

Baltic Sea hydrography – stratification and ventilation

The Baltic Sea is one of the largest semi-enclosed water bodies in the world. Its present state of an intracontinental dilution basin developed approx. 8000 years ago with the beginning of the current interglacial period. The total area of 410,000 km^2 is surrounded by a 1,745,000 km^2 drainage basin with a total mean river runoff of about 15,000 $m^3\ s^{-1}$ (Bergström and Carlsson, 1994). Higher precipitation than evaporation further contributes to the net input of freshwater into the low saline surface water. The exchange of water with the North Sea through the Kattegat - Skagerrak area in the south west is hindered by narrow straits (Little Belt, Great Belt and Sound) and shallow sills (Darss and Drogden Sill) (Fig. 1).

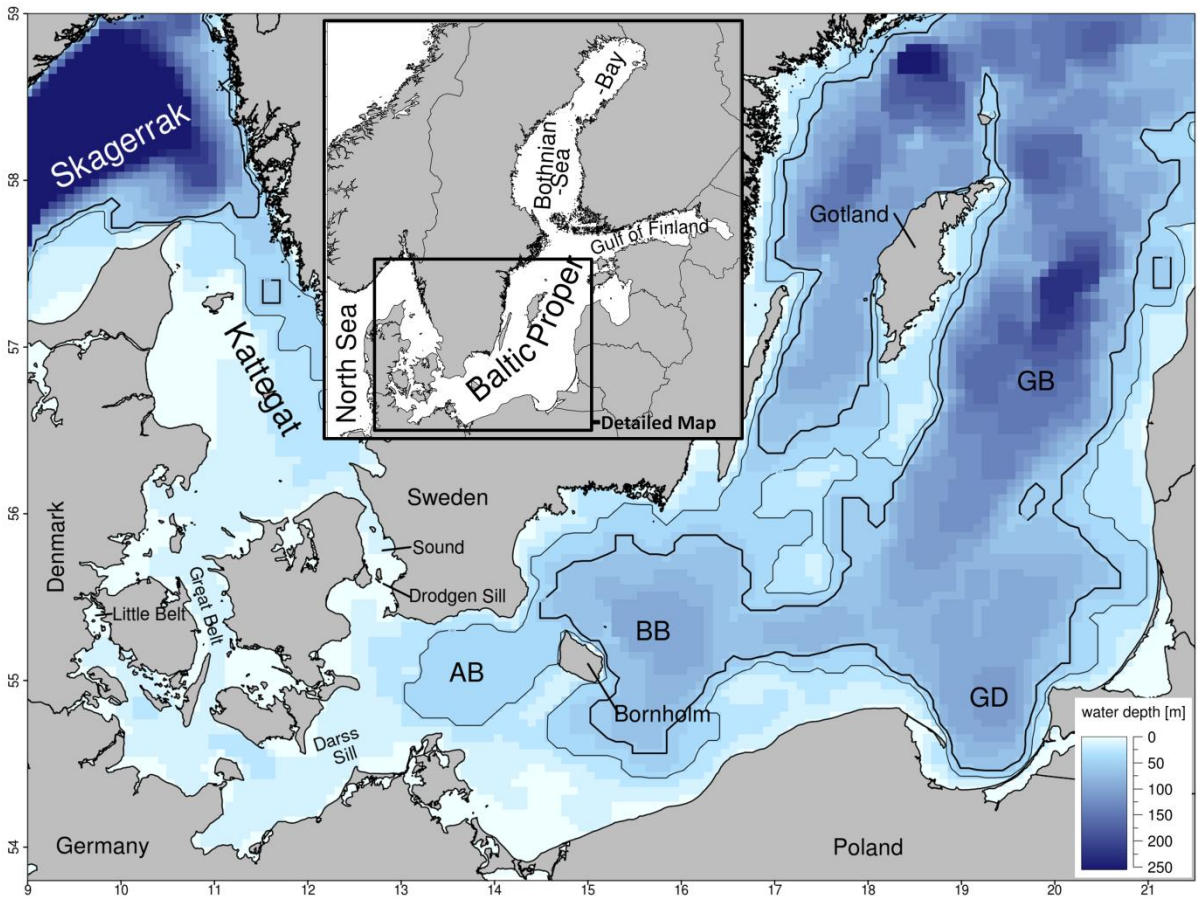


Figure 1: The western and central Baltic Sea with the main sub-basins, Arkona Basin (AB), Bornholm Basin (BB), Gdansk Deep (GD), and Gotland Basin (GB). Contour lines are 40 m (light gray) and 60 m (dark gray) isobaths.

The surplus of freshwater is therefore concentrated on the opposite north-eastern end of the Baltic Sea (Bothnian Sea/Bay and Gulf of Finland) and creates a horizontal salinity gradient with decreasing values from south-west to north-east. The density differences between the large fresh water influx and the highly saline water inflow from the North Sea create additionally an extraordinarily stable pycnocline (Stigebrandt, 1987a). The light brackish water on the surface intermixes only slowly through the general processes of breaking of internal waves (Reissmann et al., 2009), diffusion (Fennel et al., 1991) and up- and downwelling (Lehmann et al., 2002) with the more saline water underneath. Internal deep-water exchange between the sub-basins of the Baltic Proper (Fig. 1) is strongly influenced by shallow sills and channels, making the dynamics and hydrographic conditions within the sub-basins rather complex (Elken and Matthäus, 2008; Fig. 2).

Within the most western sub-basin, the relatively shallow Arkona Basin, we find both stratified and well mixed conditions over time, because high saline water can pass by advection to the deeper sub-basins further east. In contrast, the central and eastern Basins of Bornholm, Gdansk and Gotland are permanently stratified (Elken and Matthäus, 2008; Fig. 1, Fig. 2). During summer a seasonal thermocline additionally separates within these basins the warm surface waters from the intermediate cold winter water (Eilola 1997; Rak and Wieczorek, 2012). The permanent halocline below is maintained by the outflow of surface water to the North Sea (Omstedt, 2004) which creates a counter current of highly

saline water on the sea floor. Hence, a small amount of highly saline water is frequently mixed into the intermediate water layers replenishing their salinity (Schinke and Matthäus, 1998; Mohrholz, 2015).

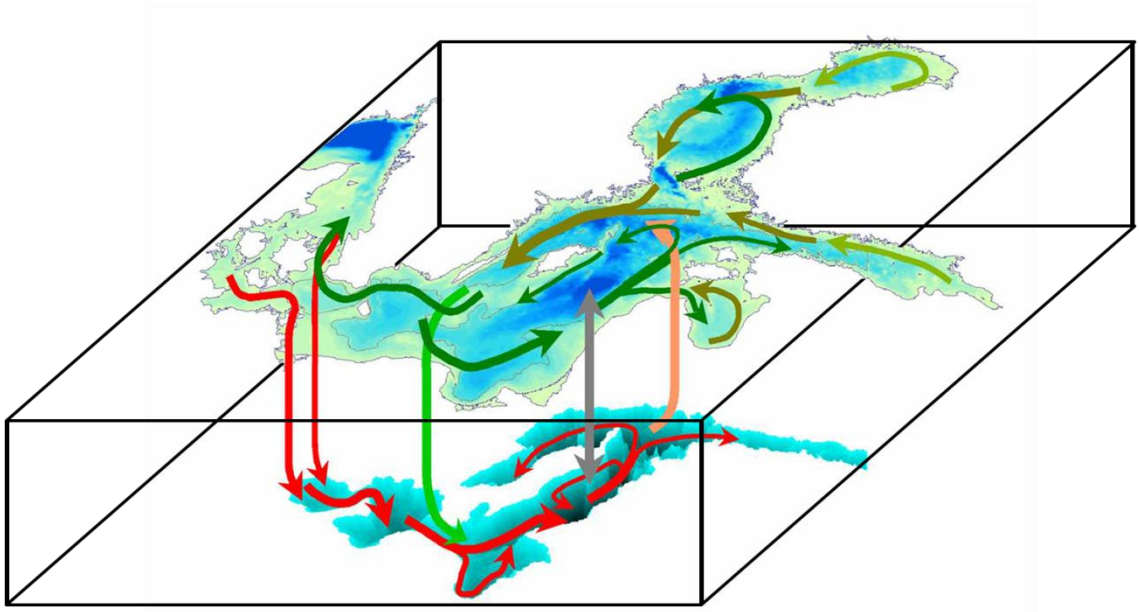


Figure 2: Large scale internal water cycle in the Baltic Sea. Red arrows indicate the path of highly saline water inflows. Arrows of dark green colors show the main surface currents, while the gray, light green and beige arrows point to the intermixing mechanisms of diffusion and up- and down-welling. Taken and slightly adapted from Elken and Matthäus (2008).

Conditions with long periods of easterly gales combined with wet winters followed by continuous westerly winds in the Kattegat area reverse the net flux through the Danish straits and force large amounts of highly saline water into the Baltic Sea (Matthäus and Franck, 1992; Schinke and Matthäus, 1998). These irregularly but reoccurring events are called Major Baltic Inflow events (MBI). MBIs are of high importance for the deep water characteristics of the Baltic Sea because only during these events the advecting water masses are of sufficient salinity and volume to be intermixed with the bottom water. Consequently, the otherwise enclosed water bodies below the permanent halocline are being reoxygenated only during MBIs (Burchard, 2009). Taken together, the respective hydrographical conditions within the sub-basins, the bathometry as well as the hydrographic properties of the inflowing water determine the distance and vertical depth on which the inflowing water travels (Lehmann and Hinrichsen, 2000). The basin sequence is however predetermined (Fig. 2). The inflowing water has to pass a narrow strait north of the island of Bornholm in order to leave the Arkona Basin and flow into the Bornholm Basin. If the volume of the MBI is relatively large it is forced to form a shallow dense pool at the bottom of the Arkona Basin (Stigebrandt, 1987b) before spilling into the Bornholm Basin, Gdansk Deep and Gotland Basin (Krauss and Brügge, 1991). How far the inflow reaches further east than the Bornholm Basin depends on the strength (water volume) of the particular MBI (Stigebrandt, 1987b). MBIs are observed during the period from August to April and are most frequent between October and February (Schinke and Matthäus, 1998). Due to these special characteristics of the Baltic Sea, water residence times within the deeper parts of the sub-basins can exceed 8 years (Meier, 2005), making it vulnerable

to anthropogenic influences (HELCOM 2007) and rendering ecosystem management strategies difficult (Blenckner et al., 2015).

Additional anthropogenic pressures

The Baltic Sea ecosystem is currently under high pressure caused by anthropogenic impacts. Overfishing (Möllmann et al., 2008; Carpenter, 2016; Voss et al., 2017), pollution (Broeg and Lehtonen, 2006), high ship traffic (Kotta et al., 2016), introduction of non-indigenous species (Ojaveer et al., 2017) and climate change (Zillén et al., 2008) have ongoing severe impacts on the ecosystem and organism level. In this regard, same as for oxygen depletion, the Baltic Sea is compared to other coastal areas far ahead. Adding to the reasoning why it was recently proposed to be used as model region to study consequences and mitigations of future-scale coastal perturbation (Reusch et al., 2018).

Poor waste water treatment and the intensified use of agricultural land within the drainage basin of the Baltic Sea during the 70's and 80's exhibited adverse effects detectable until the present day (Gustafsson et al., 2012). High nutrient input fostered degradation of organic matter by heterotrophic organisms in the bottom water (Melzner et al., 2012) and resulted in high oxygen depletion rates. The strong stratification prevented ventilation through the surface and the frequency of MBIs slowed down drastically during a transition period from 1976 to 1983. Before 1976 MBIs were observed regularly every 2 to 3 years, whereas between 1983 and 2015 the only significant MBIs were observed in 1993 and 2003 (Mohrholz et al. 2015). Hence, hypoxic areas on the sea floor expanded heavily and could be observed frequently since 1983 in most deep parts of the Baltic Proper (Fig. 3). As a consequence, species' distributions and compositions in mid and deep waters in the Baltic Sea were heavily impacted (Carstensen et al., 2014). Thus, coastal eutrophication and the resulting hypoxic areas are currently considered to be among the most severe threats to the Baltic Sea ecosystem (Andersen et al., 2017; Reusch et al., 2018). The HELCOM action plan addresses this issue and most coastal states agreed to significantly reduce the yearly net input of nutrients (mainly nitrogen (N) and phosphorus (P)) and set the goal to bring the Baltic Sea to a state of "not affected by eutrophication" by 2021 (HELCOM, 2007). These efforts were able to reverse the trend of increasing nutrient inputs and a significant decline was observed over a period of 15 years (Gustafsson et al., 2012). However, the Baltic Sea action plan targets were not able to be met and the yearly additional input currently reached a plateau of approx. 12% N and 50% P above the target (Reusch et al., 2018). Due to, the long retention time of nutrients in the Baltic Proper a new equilibrium is only to be expected by approx. 2070 (Gustafsson et al., 2012). Therefore, the reduction will most likely be not sufficient to significantly reduce the overall eutrophication state of the system and eutrophication induced pressures and hypoxic areas are still and will be imminent threats for species' habitats in the Baltic Sea.

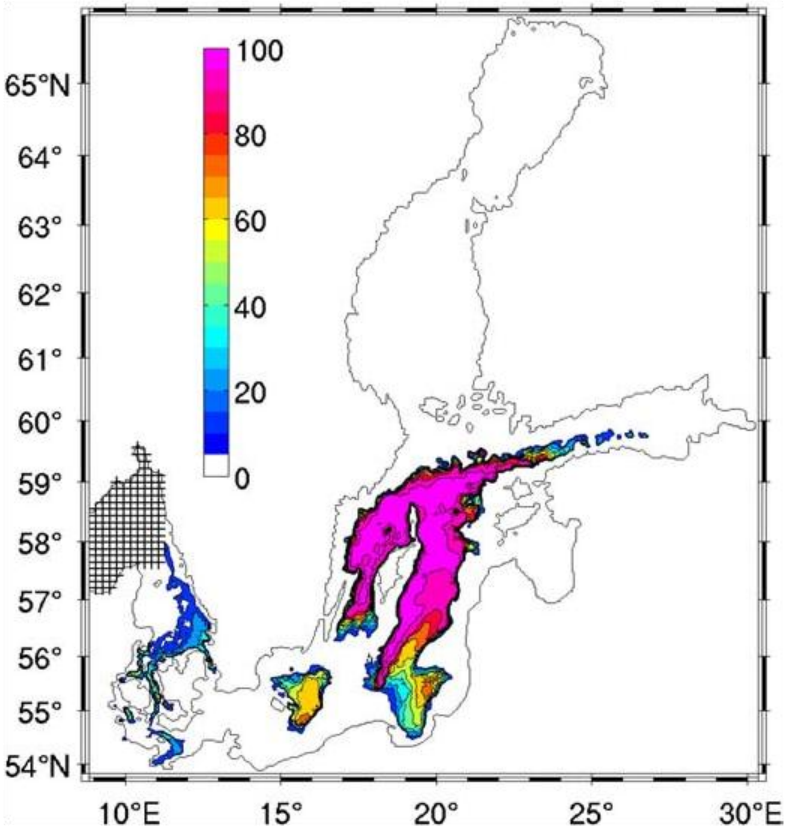


Figure 3: Frequency of hypoxia ($O_2 \leq 2$ ml/l) in the Baltic Sea for the period 1970–2010. Taken from Lehmann et al. (2014).

Oceanographic modeling and model frameworks

The physical and biogeochemical processes that govern the most important abiotic drivers in the Baltic Sea, stratification and oxygen content, are well understood and can be described by physical and biogeochemical models. However, while physical oceanographic mechanisms can be simulated in sufficient detail in numerical mechanistic models, simulating biogeochemical mechanisms is still challenging (Conley et al., 2002). Hence, there are profound uncertainties within the existing biogeochemical models due to the complexity and interaction of mechanisms and unknown initial conditions such as nutrient content in river run off, sediment fluxes and turnover rates of relevant substances in the sediment (Lehmann et al., 2014). Recent advances in coupled physical-biogeochemical models incorporating models that were developed for sediment nutrient fluxes, yield good results (Radtke et al., 2018). These models are however regionally very limited and show weaknesses within parts of the parameterization that lead to wrong estimations in extreme conditions (Radtke et al., 2018). A model framework for the entire Baltic Sea incorporating all known mechanisms determining the oxygen characteristics, which could provide a quasi-synoptic and observationally validated view on the entire model domain does not yet exist. To investigate on the biological impacts of oxygen depletion, map species habitats and develop environmental indicators for ecosystem management a high resolution data base and a framework for explorative modelling exercises is needed.

Within my PhD thesis, I therefore used the established mechanistic numerical ocean model BSIOM (Baltic Sea Ice-Ocean Model; Lehmann, 1995; Lehmann & Hinrichsen, 2000;

Lehmann et al., 2002) instead of the defective biogeochemical models. It employs atmospheric forcing to model in hindcast all oceanographic processes below the sea surface, which govern temperature, salinity and current velocity in the system. Oxygen conditions were simulated by a simplified oxygen sub-model, which reflects the overall primary production development in the Baltic Sea (Lehmann et al., 2014). It further applies sub-basin depending oxygen depletion rates that were modulated by functions driven by current oxygen content and temperature. This model frame work captures the intra-annual variations and dynamics of the system sufficiently to be used in detailed analyses of ecological and environmental interactions (e.g. Lehmann et al., 2014; Hinrichsen et al., 2011, 2012). Biogeochemical processes are however mostly neglected. Therefore, process studies and budget calculations are not possible. Nevertheless, in my thesis, I used BSIOM as a high resolution data base for studies of habitat characteristics and spatio-temporal developments. Furthermore, I realized a particle tracking method, which was based on the detailed velocity fields obtained by the model. Lagrangian drift routes were compiled by calculating the advection of marked water particles. With this technique it is possible to assess complex drift patterns and long-term drift-off dynamics of passively drifting life stages like fish eggs and larvae (Hinrichsen et al., 2003).

Hence, the used BSIOM model framework was able to deliver the data basis for the analyses conducted in my thesis. Although highly resolved in situ measurements and detailed plankton recordings would be ideal to perform ecological studies on drift patterns of early life stages and environmental impact studies, the current data situation requires the support by ocean model frameworks (e.g. Tedesco et al., 2016; Pecuchet et al., 2014; Fulton, 2010). This holds especially true, when general drift patterns or abiotic conditions and detailed dynamics of the system of ecological relevance are to be studied and in-situ measurements are not sufficient in resolution and /or time extension (von Dewitz et al., 2018). Here, BSIOM is a satisfactory source of high resolution 3D data for salinity, temperature and oxygen for the entire Baltic Sea, which does not divagate in the biogeochemical processes that are not yet possible to simulate at this scale.

Eastern Baltic cod

In my thesis, I focused on Eastern Baltic cod (*Gadus Morhua*) since it is one of the ecologically and economically most important demersal (and pelagic) species in the Baltic Sea. The species is of marine origin and shares the highest trophic level in the system with seals and predatory sea birds. Out of more than 40 fish species cod, herring and sprat are the most abundant fish populations in the Baltic Sea. Many studies on the ecosystem level are focusing on these three species to investigate mechanisms regarding fisheries biology (e.g. Casini et al., 2011), ecology (e.g. Harvey et al., 2003) and economy (e.g. Nieminen et al., 2012).

Eastern Baltic cod is distributed throughout the Baltic Sea Proper (Fig. 1) and also shares its habitat with the distinct western population in the Arkona Basin area (Bagge et al., 1994; Berg et al., 2015). The population is however concentrated in the southwest of the Baltic Proper with the Bornholm Basin as distribution centre (Bartolino et al., 2017). Foraging is done over widely spread areas from the deeper basins up to shallow coasts throughout the year intensifying outside the spawning season during winter and spring

(Bagge et al., 1994). The diet juveniles and adults includes pelagic and benthic invertebrates, most importantly *Sarduria entemon* and *Mysis spec.*, and fish, mostly clupeids (Bagge et al., 1994; Huwer et al., 2014). Spawning habitats are restricted to the deeper basins (Bagge et al., 1994) which usually provide sufficiently high salinities for the pelagic eggs to be neutral buoyant in the water column (von Westernhagen, 1970; Wieland, 1995). After 3 to 4 weeks (~110 degree-days) of development the larvae hatch and stay largely inactive in the water column (Grønkjær and Wieland, 1997) until they switch to active feeding when the mouth opens ~3 days post hatch, while the yolk sac is depleted at ~5 days post hatch (Falk-Peterson, 2005). During this period a migration to the upper water layers takes place where the larvae feed visually on zooplankton (Grønkjær and Wieland 1997, Huwer et al., 2011) until they reach the metamorphic phase in which they settle onto the sea floor in shallower regions (Hüssy et al., 1997; Casini et al., 2016). In these nursery areas, benthic prey is the main diet of the juveniles. When the individuals reach body lengths of over 20 cm they start to include also fish into their diet (Huwer et al., 2014; their figure 2). Due to a high fishing mortality for individuals larger than 35 cm, length at 50% probability of maturing has been decreasing in both sexes during the last 3 decades by about 20% to approx. 20 cm (Vainikka et al., 2009; ICES, 2016). During one spawning cycle females release 12-16 batches of eggs resulting in a size depending potential fecundity between 400,000 (first time spawner) and over 8 million eggs (Vallin and Nissling, 2000). During spring the individuals develop ripening gonads and migrate to the deep basins to spawn between March and September (Köster et al., 2016). Males mature earlier and stay fertile during most of the spawning period (Tomkiewicz and Köster, 1999), whereas females spawn their batches only over a few weeks (~ 50 days), before a resting stage is entered (Kjesbu, 1989). The spawning activity varies temporally among individual females (Bleil and Oberst, 1998; Bleil et al., 2009). The peak spawning activity of the entire stock was observed to have changed during the last few decades from April to June in the 1970s and 1980s (MacKenzie et al., 1996) to the end of July in the 1990s (Wieland et al., 2000; Bleil et al., 2009) and again to a more evenly spread utilization from May to August in the 2000s (Baranova et al., 2011).

Impact of abiotic drivers on early life stages of Eastern Baltic cod

During ontogeny abiotic drivers impact the survival of eggs, larvae and juveniles, determining the recruitment success of the population at large. For a successful fertilization, adequate abiotic conditions are essential. A salinity of at least 11 is needed in order for the spermatozoa to be activated and thereby being enabled to penetrate the eggs chorion (Nissling and Westin, 1997). Subsequently, the fertilized eggs need to achieve neutral buoyancy in the water column to avoid the lethal bottom contact (Wieland et al., 1995). At this stage the water density, determined mainly by salinity content at the spawning location, has to match the eggs density. Eastern Baltic cod eggs are adapted to the brackish Baltic Sea and therefore achieve neutral buoyancy at lower salinities than their Atlantic counterparts (Grauman, 1973). However, egg buoyancy is dependent on female size (Vallin and Nissling, 2000) since female size determines the egg diameter, which in turn correlates with egg density (Petereit et al., 2014). This causes a large range of egg buoyancies to be observed in the field (Hinrichsen et al., 2016). Due to these facts, my

thesis considers for the first time female size in the efforts to map and classify the spawning habitat of Eastern Baltic cod. Due to the oxygen stratification of the water column the depth of neutral buoyancy determines the oxygen content experienced by the eggs (Hinrichsen et al., 2016). Cod eggs need at least 2 ml/l oxygen in order to have a chance to develop and hatch (Wieland et al., 1994). However, at this minimum the chances of survival are already heavily reduced. Based on experimental studies Köster et al. (2005) developed a model which I used in my thesis to relate survival chances to a certain oxygen content.

With first feeding and the associated vertical migration oxygen plays a crucial role in order to sustain an active upwards swimming behaviour from the depths of the egg stages of >50 m (Rohlf, 1999), because most suitable prey is located in depths of the euphotic zone between 10 -30 m (Huwer et al., 2011). During the larval phase, cod is in need of a constant supply of meso-zooplankton organisms, i.e. mainly copepodid stages of the calanoid copepods *Acartia* spp. and *Pseudocallanus* spp. (Voss et al., 2003). The abundances of these species are mainly driven by abiotic conditions and the availability of food, suitable primary producers, which is as well heavily depending on abiotic drivers (Hinrichsen et al., 2002).

After metamorphosis to juveniles cod need to settle in shallower regions where the prey is abundant (Hüssy et al., 2003); and oxygen conditions at the sea floor are sufficient to sustain their metabolic rate (Chabot and Dutil, 1999) as well as a vital benthic community (Hinrichsen et al., 2003). The larval transport to a suitable habitat and the successful settlement is driven by wind and other drivers of ocean currents. Once settled, they serve as prey for many species large enough to hunt them, including larger cod (Uzars and Plikshs, 2000). The availability of suitable areas, needed to sustain a high abundance of juveniles, is therefore one bottleneck for juvenile survival and the extent of these areas is determined by the salinity and oxygen conditions (Köster et al., 2009; Casini et al., 2012).

Environmental factors for quantifying cod reproduction habitat

Over the last 20 years, factors representing abiotic forcing and other environmental considerations were increasingly included into research of reproduction success (Möllmann et al., 2011) which led to the current view that an integrated ecosystem approach is needed for fish stock management (Möllmann et al, 2013). One of the first attempts to relate the environmental conditions to reproduction success was the introduction of the Reproductive Volume concept (RV) by Plikshs et al. (1993) (see Fig. 4 for illustration). It focuses on the environmental spawning conditions for Eastern Baltic cod and incorporates the tolerance levels for oxygen and temperature (O_2>2 ml/l, T >1.5°C) available at that time. Further it incorporates the minimum salinity of 11 needed to sustain neutral egg buoyancy introduced by Grauman et al. (1973). Due to strong inverse correlation between salinity and oxygen content in the Baltic Sea (Fig 4) large RVs in the Bornholm Basin could be linked to a successful reproduction (MacKenzie et al., 2000).

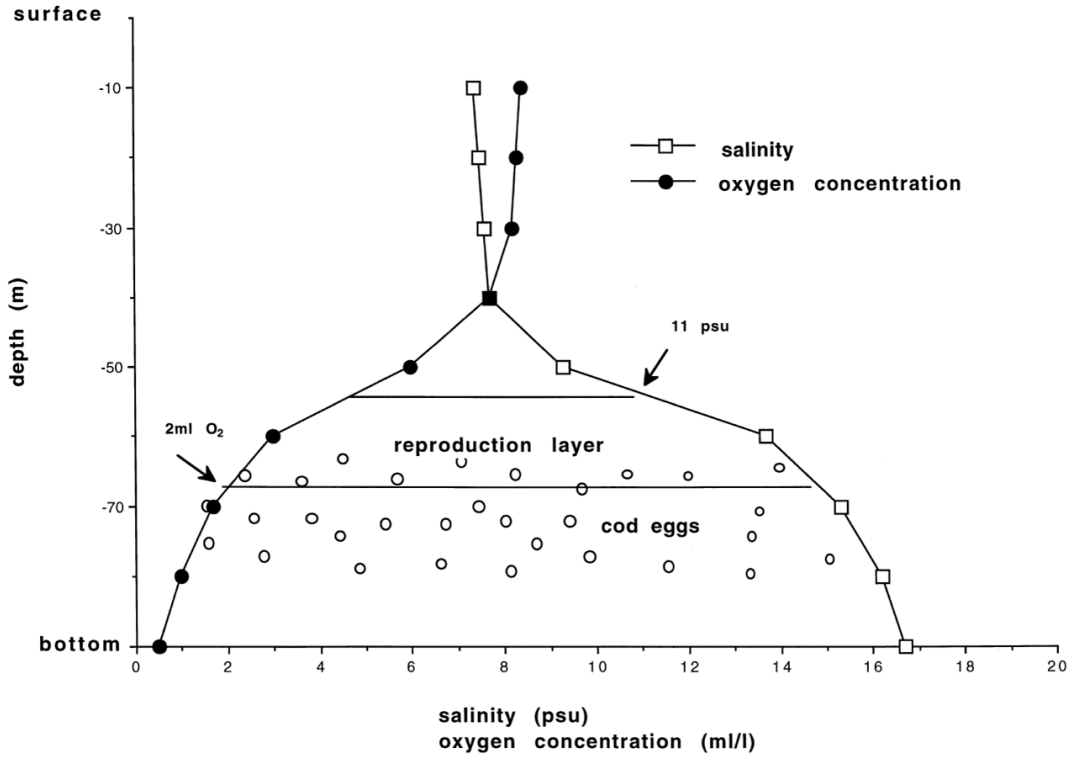


Figure 4: Schematic view of the hydrographical conditions in the Bornholm Basin. Shown are typical vertical profiles of salinity and oxygen content. Horizontal lines represent the boundaries of the Reproductive Volume (S > 11, O2 > 2 ml/l) after the definition from MacKenzie et al. (2000). The area where cod eggs are distributed represents the average salinity of neutral egg buoyancy (S = 14.5 ± 1.2) according to Nissling et al. (1994). Taken from Vallin and Nissling (2000).

Following these first efforts, variations of the RV were also suggested as useful environmental factors in regard to cod reproduction, i.e. the depth of the 11 isohaline and a one point measure of the thickness of the RV in the middle of the Bornholm Basin (all reviewed in Köster et al., 2016). However, putting a minimal salinity of 11 at the centre of the efforts proved to be premature. Further research showed, that (1) egg buoyancy in the field has a large variation (Hinrichsen et al., 2016), (2) egg buoyancy is female size dependent (Vallin and Nissling, 2000) and (3) the minimum salinity needed to sustain egg buoyancy is most probably higher than 11 (Nissling and Vallin, 1991, 1996, 1997). Furthermore, the correlation between oxygen content and egg survival is not a sharp cut off from 100% survival to 0% below 2 ml/l O_2 but follows a sigmoid curve (Köster et al., 2005) and the sub-basins show strongly heterogenic vertical oxygen distributions, making a large RV not necessarily an indication for good reproduction conditions in all depths. Köster et al. (2001) attempted to incorporate the vertical depth distribution of cod eggs from ichtyoplankton sampling into egg survival estimates. However, here the connection to female size depending egg buoyancies was not made and therefore the dependency of recruitment from stock structure (Cardinale and Arrhenius, 2000) was not able to be incorporated which I attempt for the first time in this thesis. Additionally, the conditions found in the Bornholm Basin and those in other sub-basins further east are not necessarily interchangeable. Research by Maris Plikshs et al. (2015) showed that for the species eastern border of distribution other concepts need to be developed. A concept, which includes quantitative and qualitative environmental conditions for the spawning grounds of

Eastern Baltic cod, incorporates the current understanding of the hydrographic system, considers size depending processes and is ready to be used in management of the stock, is still missing. Hence, in my thesis, I aim to close this gap by developing such a concept, testing it against existing concepts and applying it to current research questions regarding the environmental impact on the Eastern Baltic cod reproductive habitat.

Thesis outline

The aim of my thesis was to improve our understanding of the impact and the dynamics of environmental drivers on the reproductive habitat of Eastern Baltic cod by using the existing process knowledge of the hydrographic system and by developing a new concept how the quantity and quality of the available spawning habitat can be assessed. I therefore developed, validated and applied a precise framework to calculate environmental indicators and evaluated the spawning habitat size and quality for Eastern Baltic cod by the approach of Buoyancy Depending Reproductive Layers (BDRL). The BDRLs are able to incorporate female size depending processes and the current knowledge base. One central aspect of my thesis was to test this concept for its relevance in the recruitment process. Furthermore, drift patterns within the spawning grounds are important to resolve larvae distributions and juvenile settlements, which need to be considered when the abundance of recruits is related to the reproduction success. Hence, I used the BSIOM to evaluate long term drift patterns and thereby assessed connectivity patterns between spawning and nursery grounds as well as the relative occupation of the limited habitat. I then further applied the BDRL concept to investigate female size dependent whether and how the spawning habitat is impacted by eutrophication and compared the BDRL-methodology with the classical RV approach. My ultimate aim was, to use the BDRL concept to provide an indicator for an integrated assessment, which considers the environmental spawning habitat characteristics. Therefore the possibility to use the procedure to inform the yearly stock assessment about environmental conditions by the means of a short term forecast or early warning indicator was assessed.

Four main working hypotheses (equivalent with H_1-hypotheses) were investigated:

(1) The BDRL approach can be used as a basis for an alternative environmental recruitment indicator, which is performing better than the current use of the Spawning Stock Biomass (SSB)

(2) Drift patterns influence the use of the limited available nursery grounds for juvenile cod and the settling success of individuals depends on the spawning site

(3) The Eastern Baltic cod spawning habitat is impacted by eutrophication and the BDRL approach performs better than the “classical” RV approach in testing such environmental impacts and dynamics of the spawning habitat

(4) The BDRL approach can be combined with existing infrastructure, i.e. the measurement platform in the Arkona Basin equipped with salinity sensors, to perform short term forecasts of the environmental spawning conditions for Eastern Baltic cod and the resulting indicator is suitable to inform advisory institutions of fisheries management

I have structured my thesis into 4 chapters. All chapters have the form of a manuscript including an Introduction, Materials and Methods, Results and Discussion part.

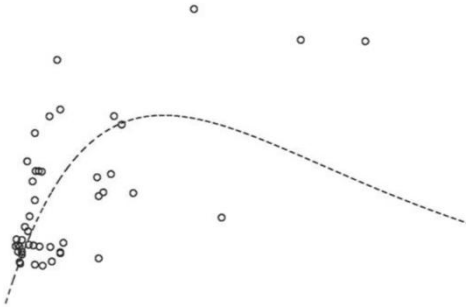
Chapter 1, entitled "Oxygen depletion in coastal seas and the effective spawning stock biomass of an exploited fish species", has been published in the journal of the "Royal Society Open Science" in 2016 and investigates on hypothesis (1). The BDRL approach was used here to establish a novel concept, the effective Spawning Stock Biomass (eSSB), which then was tested within a recruitment model against a model without any environmental considerations.

Chapter 2, entitled "Spatio-temporal dynamics of cod nursery areas in the Baltic Sea", has been published in the journal of "Progress in Oceanography" in 2017 and investigates on hypothesis (2). It studies the long term dynamics of the habitat occupation within the available nursery grounds and the relative importance of the sub-basins as origin of successful settled juveniles by the means of drift modelling.

Chapter 3, entitled "Hindcasting the sensitivity to eutrophication of the Eastern Baltic cod (*Gadus morhua*) spawning habitat", investigates on hypothesis (3) and is currently being reviewed by my co-authors before it will be submitted to the journal "PLoS ONE". It compares the BDRL approach with the common RV approach by using both concepts to investigate on the impact of eutrophication and other relevant research questions regarding the spawning habitat of Eastern Baltic cod.

Chapter 4, entitled "Use of existing hydrographic infrastructure to forecast the environmental spawning conditions for Eastern Baltic Cod", has been published in the journal "PLoS ONE" in 2018 and investigates on hypothesis (4). Here the possibility is tested weather the BDRL approach can be used to develop a short-term prediction / early warning indicator for the spawning habitat quality to inform the yearly stock assessment.

Chapter 1



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Oxygen depletion in coastal seas and the effective spawning stock biomass of an exploited fish species

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Abstract

Environmental conditions may have previously underappreciated effects on the reproductive processes of commercially exploited fish populations, for example Eastern Baltic cod that is living at the physiological limits of their distribution. In the Baltic Sea, salinity affects neutral egg buoyancy, which is positively correlated with egg survival, as only water layers away from the oxygen consumption-dominated sea bottom contain sufficient oxygen. Egg buoyancy is positively correlated to female spawner age/size. From observations in the Baltic Sea a field-based relationship between egg diameter and buoyancy (floating depth) could be established. Hence, based on the age structure of the spawning stock, we quantify the number of effective spawners, which are able to reproduce under ambient hydrographic conditions. For the time period 1993-2010, our results revealed large variations in the horizontal extent of spawning habitat (1000 to 20000 km^2) and oxygen-dependent egg survival (10 to 80%). The novel concept of an effective spawning stock biomass takes into account offspring that survive depending on the spawning stock age/size structure, if reproductive success is related to egg buoyancy and the extent of hypoxic areas. Effective spawning stock biomass reflected the role of environmental conditions for Baltic cod recruitment better than the spawning stock biomass alone, highlighting the importance of including environmental information in ecosystem based management approaches.

Introduction

Large-scale expansion of oxygen minimum zones (OMZ) in marine systems and large lakes was observed worldwide over the past decades and it is a challenging task to predict future impacts on fish stocks and their ecosystems [1, 2]. Oxygen reduction could lead to widespread mortality [2] or avoidance of affected areas [3, 4, 5]. Thus, OMZ may have detrimental effects on the reproductive processes of mass-spawning, commercially exploited fish populations. OMZs will have major ecological and economic implications in the future [6] and are expected to further increase as an aspect of global climate change, in particular in Northern latitudes including the Baltic Sea [2, 7, 8].

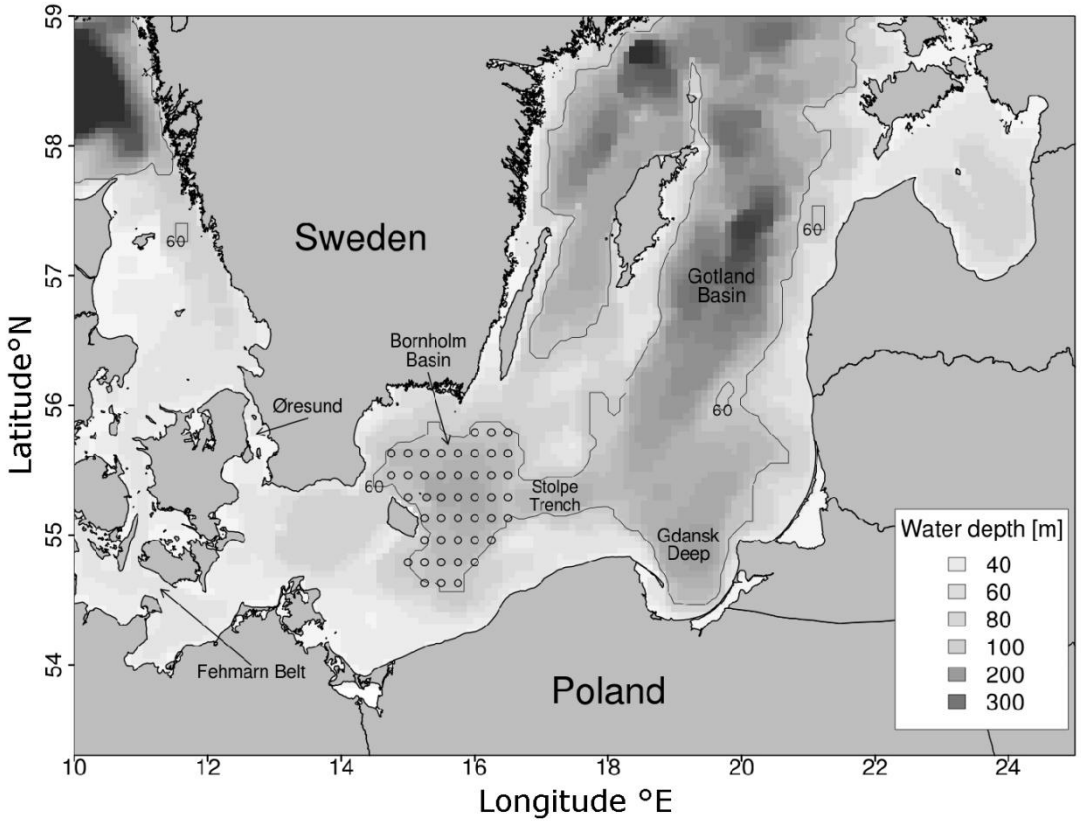

Figure 1: Map of the Baltic Sea with standard station grid in the Bornholm Basin (45 stations).

A typical example for a semi-pelagic fish stock in coastal habitats suffering from oxygen reduction is the Eastern Baltic cod (*Gadus morhua*) population. This stock is historically the third largest Atlantic cod stock [9] with a long-term mean spawning stock biomass between 1966 and 2012 of about 240.000 tons [10]. The Eastern Baltic cod stock spawns in the major deep basins (Bornholm Basin, Gdansk Deep and Gotland Basin), which are characterized by a permanent haline stratification [11, 12]. The principle mechanism causing replenishment of oxygen in these deep Baltic Sea basins is the ephemeral nature of "Baltic inflows" [13] of high saline oxygen rich water masses from the North Sea. Due to the effect of human induced eutrophication and climate-induced less frequent inflow events, the oxygen conditions in recent decades became less favorable and hypoxic areas have expanded [14]. A corresponding environmentally dependent low recruitment success

combined with high fishing pressure resulted in a reduction of the spawning stock biomass of Eastern Baltic cod from almost 650.000 to 87.000 tons from 1983 to 1992.

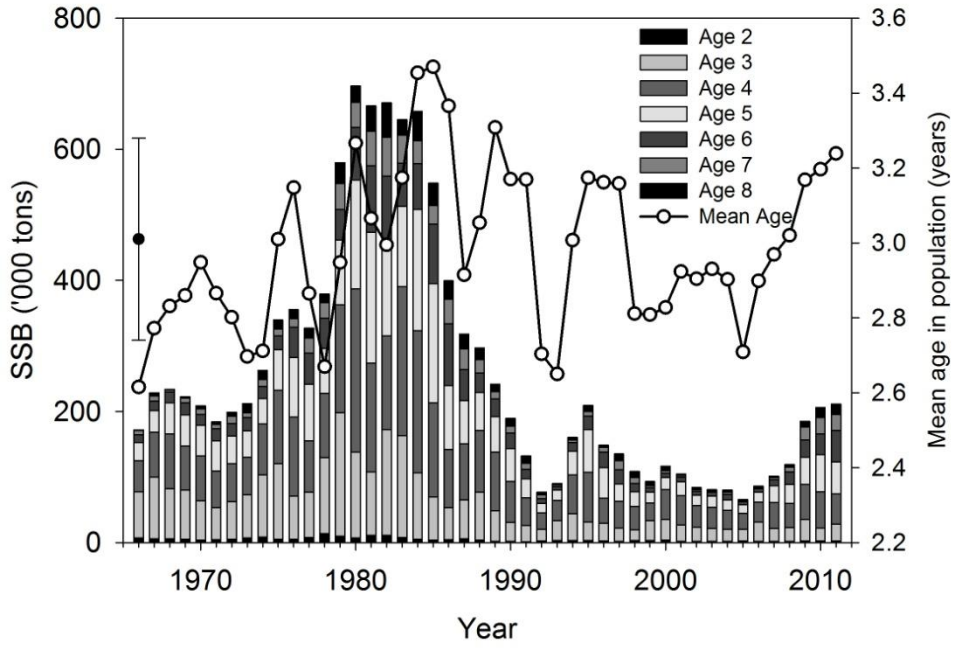

Figure 2: Baltic cod spawning stock, its age composition and mean age 1966 – 2012. The symbol to the left indicates mean age and standard deviation over the investigated time period.

Many marine fish species including cod in the Baltic Sea are living at the physiological limits of their distribution, due to the strong gradient from fully marine salinities in the Western Baltic to brackish water salinities in the North-East. For example, salinity is correlated with neutral egg buoyancy [15]. Neutral buoyancy for Baltic cod eggs is found at salinities which typically occur from below the halocline to the bottom water [16-18].

The interaction between egg buoyancy (i.e. floating depth) and oxygen concentration is important for the survival of eggs of different species in the Baltic Sea [16, 19]. Specifically, due to the hydrography of the Baltic Sea, the development of more buoyant eggs occurs in more favorable oxygen conditions. Egg buoyancy is positively correlated to egg diameter, which in turn is influenced by spawner characteristics. Kjesbu and colleagues [20, 21] showed a highly significant positive correlation between egg diameter and female size for Atlantic cod. For Baltic cod several experimental studies confirmed that large, older females on average produced larger eggs with neutral buoyancy at lower salinity (water density) compared to smaller eggs spawned by smaller, younger females [22, 16]. Although egg size also varies within a batch, and between batches produced throughout the spawning season, larger more buoyant eggs spawned by larger (older) females [23] are hence expected to have on average higher egg survival probability.

The here presented approach follows the need to inform Integrated Assessments and Ecosystem-based Management [24]. Within this context analyses on the state and development of the various Baltic ecosystems have been conducted [25-28]. The ICES Working Group on Integrated Assessments of the Baltic (WGIAB) has successfully performed integrated trend and status assessments which have been used for developing a

set of ecosystem indicators that can support the assessment of the stock status of individual species [29]. Individual indicators were evaluated for showing support for or against the assessment model-derived stock status and trends.

Table 1: Mean egg density (averaged over all spawning batches) for female spawners of different age [23].

Age class	Egg density
8	1010.00±1.11
7	1010.71±0.85
6	1010.95±0.84
5	1011.25±0.82
4	1011.61±0.81
3	1012.06±0.42
2	1012.71 ± 0.40

Here, we provide the first comprehensive, field-based evidence for the link between cod egg size and floating depth. We then quantify and visualize the stock-structure effect on spawning area extension, the ambient oxygen concentration experienced by eggs as well as egg mortality for contrasting environmental conditions (i.e. post-inflow vs. stagnation). In a third step, we calculate time series of oxygen-related cod egg survival probability for the entire spawning periods from 1993 to 2010. Finally, we develop and test the concept of effective spawning stock biomass (eSSB) as an indicator of recruitment potential, which is integrating biomass, stock-structure and environmental conditions, with the Eastern Baltic cod stock as an example.

Materials and Methods

Field validation

In order to confirm a laboratory-derived correlation between egg size and floating depth (i.e. water density) for variable hydrographic conditions in the field, vertically resolved sampling was conducted during 7 RV "Alkor" cruises between 2002 and 2010 The vertical distribution of cod eggs was investigated with a towed multiple opening-closing net at selected stations with large numbers of cod eggs as derived from Bongo net samples (Fig. 1). The gear in use was a HYDROBIOS MAXI-type Multi net (Hydrobios, Holtenau, Germany) with a net mouth opening of 0.5 m^2 equipped with net sets with 335 µm mesh size. At each station, depth profiles covering the whole water column from the surface down to near bottom were sampled in 5 m intervals. Samples were preserved in 4% buffered formaldehyde/seawater solution immediately after collection, and cod egg diameters (in 0.025 mm size classes) were subsequently measured for at least 100 eggs per sample. Weighted mean egg diameters per sample were then calculated and assigned to mean ambient water densities/egg buoyancies as derived from hydrographic measurements with a CTD-probe (conductivity, temperature, depth) taken at each of the sampling stations. As a next step, from a total of 150 multi net samples, average egg diameters were correlated to water density (measured in classes of 0.5 kg m^{-3}).

Quantification of the spawning environment and egg mortality

To calculate the spatial extent of the spawning environment, hydrographic data (temperature, salinity, oxygen concentration) were compiled from 54 cruises in the Bornholm Basin between 1993 and 2010. The surveyed area displayed by the station grid in Fig. 1 covers the area enclosed by the 60 m isobaths, which represents the historical peak egg and larval abundance area of Baltic cod in the Bornholm Basin [30]. The cruises consisted of a total of 45 standard stations, with a horizontal resolution of 8 to 10 nautical miles. In only a few years, not at all stations hydrographic measurements were available, mainly due to bad weather conditions. However, a sufficient horizontal coverage of hydrographic properties for further analyses could be achieved for all years. Based on hydrographic parameters measured at the standard station grid, for each cruise we calculated the 3-dimensional extension of the spawning volume. As obtained from field observations as well as from laboratory experiments for Eastern Baltic cod, a minimum salinity level of 11 psu is required for neutral egg buoyancy, whereas eggs at lower salinities sink to the bottom and die. At the same time, a minimum oxygen level of 2 ml l^{-1} and temperatures above 1.5°C are required for eggs to develop successfully [17-18, 31].

We displayed the horizontal distributions of the spawning conditions for different levels of egg buoyancy, which is associated with female spawner size. The distributions were estimated with an objective analysis [32]. This method is designed for data sets containing relatively low numbers of observations and is able to interpolate across stations where no data could be assigned. It is based on a standard statistical approach, the Gauss-Markov theorem, which gives an expression for the linear least-square error estimate of the variables. The method creates horizontal fields representing the spawning conditions by interpolating the associated observed environmental parameters onto a regular grid (see Appendix 1, equation 1). The method can make use of statistics with respect to measurement errors and small-scale noise inferred from the observed data. Thus, at single locations an estimate can be given that depends linearly on the total number of measurements, i.e. a weighted sum of all observations. Based on repeated observations at individual stations, it was obtained that the error due to measurement errors and small scale noise amounts to 15% of the total variance of the abundance fields and that these errors are normally distributed. As most of the surveys were designed to produce quasi-synoptic horizontal fields of the Baltic cod spawning conditions, a unit array configuration with a horizontal resolution of 5 km was chosen and superimposed on the standard station grid. Hereby, each of the grid points is representative of the analyzed properties around it. However, only areas were considered where the expected root mean square of the interpolation was < 50% of the standard deviations of the observed property fields. Generally, the objective analysis method provides a smoothed version of the original measurements, with a tendency to underestimate the observed values. This is due to the specific assumptions made regarding our treatment of measurement noise and small-scale signals unresolved by the meso-scale observation array. The error estimates depend mainly on the statistics of the field, the noise level, and on the locations of the observations, but not on the measurements themselves.

Oxygen-dependent survival probability maps were constructed for those density levels where cod eggs in the Baltic Sea are typically neutrally buoyant.

Horizontal maps and time series data on the cod spawning habitat characteristics were assembled for different buoyancy levels (1009, 1011, 1013 kg m^{-3} , corresponding to ca. 11, 13.5 and 16 psu at a temperature of around 5°C). These levels were chosen to represent the buoyancies of eggs of different female age categories: old (large), mid-age (medium size) and young (small) cod, and were based on the results described in [23].

Calculation of effective Spawning Stock Biomass (eSSB)

We used the information on variable egg mortality depending on spawner-age and hydrographic conditions, to derive a new time-series of 'effective' spawning stock biomass (eSSB). This new time-series can be seen as a derivative of stock reproductive potential and mirrors the effect of variable age-distribution in the spawning stock in combination with variable hydrographic conditions on recruitment; it is tested and used in a stock-recruitment model. We tested which stock-recruitment function yielded the best fit for the traditional SSB estimates and the full time-series 1966-2012. The Ricker-type model fitted the data best, being, however, only slightly better than the Beverton-Holt or the smoothed hockey stick model. Cod cannibalism [33] as well as food competition [34] also suggests a density-dependent model. Therefore, we concentrated on the Ricker model. Because in our analysis we were not able to account for all factors contributing to variations on the female size/egg buoyancy structure (see above), we calculated simplified egg buoyancy levels (averages over all spawning batches) for each female age-class based on experimental studies [23], using data for peak spawning time (Table 1).

For the time-series 1951-2012 we then calculated oxygen-dependent egg mortality for each year and each female spawner age-class in May. Ambient oxygen contents were derived from the ICES hydrographic database and were inserted into an egg-survival function [35] based on experimental data (Equation 2 in the Appendix2).

Hydrographic conditions in the depth range of floating cod eggs are mainly influenced by irregular inflow events of North Sea water. Inflowing waters replenish the oxygen content below the permanent halocline and hence are positive for cod egg survival. Due to fast oxygen consumption caused by breakdown of organic material, good, post-inflow conditions usually last for only one year, i.e. the following year faces bad oxygen conditions again. Taking these hydrographic features into account, we divided the historic time-series in 'good' versus 'bad' condition years (and therefore high and low cod egg survival). Mean age of the historic age distribution of the stock from 1966-2012 (Fig. 2) was 3.0 ($\pm$0.3) years, showing variations between 2.6 and 3.5 years. Therefore we used egg survival at age 3 as distinctive feature, with egg survival >50% classifying a good' year and egg survival <50% classifying a 'bad' year. This resulted in a bimodal distribution, with 44 years being classified as 'bad' and 16 years with egg survival >50% (Fig. 3), classified as 'good' years.

For each of the two sets of years, we calculated mean age-specific egg survival (Table 2).

To calculate the eSSB time-series, we used relative egg survival as weighting factor for potential recruitment contribution. The factor would be = 1 at 100% egg survival. All age-

classes showed lower potential egg survival and received weighting factors between 0.861 (age-class 8+ under good conditions) and 0.017 (age-class 2 under bad conditions). For more detail see Appendix3.

Results

Cod egg mean diameter showed a strong negative correlation (r=-0.96) with the mean water density at which eggs were present in the field (Fig. 4), suggesting that egg diameter is directly associated with neutral buoyancy. This confirmed that laboratory-derived results are also applicable in the field, even under highly variable hydrographic conditions.

The horizontal maps showing the Baltic cod spawning habitat extension and corresponding oxygen-related cod egg survival revealed (i) strong differences in suitable habitat related to the different buoyancy levels, and (ii) strong temporal fluctuations related to environmental variability (Fig. 5) between a major Baltic Inflow situation in April 2003 and a stagnation period in May 1997. Specifically, after the major Baltic Inflow in 2003 the areas related to the selected buoyancy levels (1009, 1011, 1013 kg m^{-3}, corresponding to ca. 11, 13.5 and 16 psu at a temperature of around 5°C) were widely extended over the whole Baltic cod spawning ground in the Bornholm Basin (17872, 16302, 8594 km^2 on the respective buoyancy level) with overall almost optimal favorable spawning conditions in terms of cod egg survival probabilities (means: 0.94, 0.83, 0.87). During the stagnation period the maps suggest a significant decrease of the extent of suitable spawning habitat (17187, 15617, 3826 km^2) at the different egg buoyancy levels associated with on average much lower egg survival probabilities (0.73, 0.52, 0.09). Average habitat extension and egg survival probabilities for the different egg buoyancy levels are summarized in Table 3.

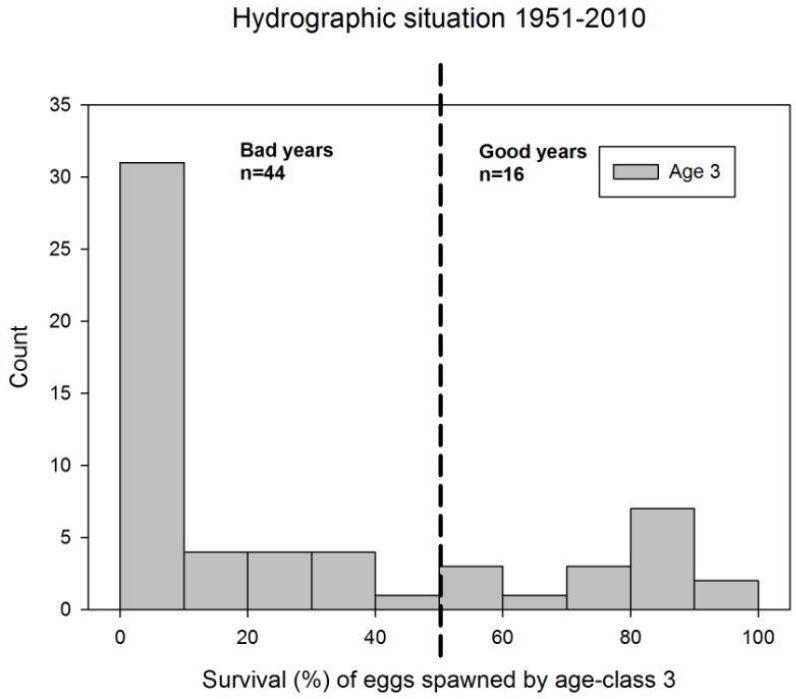

Figure 3: Survival of eggs spawned in May by age-class 3 in 1951 – 2010. Years with egg survival >50% ('good' years, n=16) are 1952, 1954, 1959, 1960, 1961, 1964, 1969, 1976, 1979, 1980, 1986, 1993, 1994, 1998, 2003.

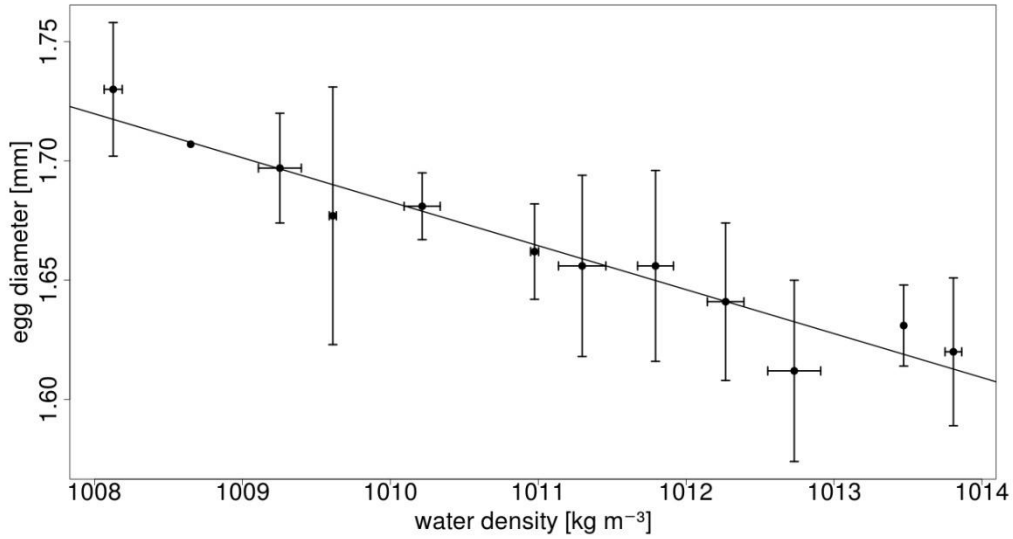

Figure 4: Mean egg diameter versus mean density of ambient seawater. Error bars represent standard deviation of mean values.

Table 2: Mean egg survival for different female age classes under good (*n*=16 years) and bad environmental conditions (*n*=44 years) out of the time series 1951–2010.

Age-class	Survival (bad)	Survival (good)
8	47.3	86.1
7	35.9	76.3
6	30.1	73.2
5	23.2	71
4	15.6	73
3	8.4	76
2	1.7	60.7

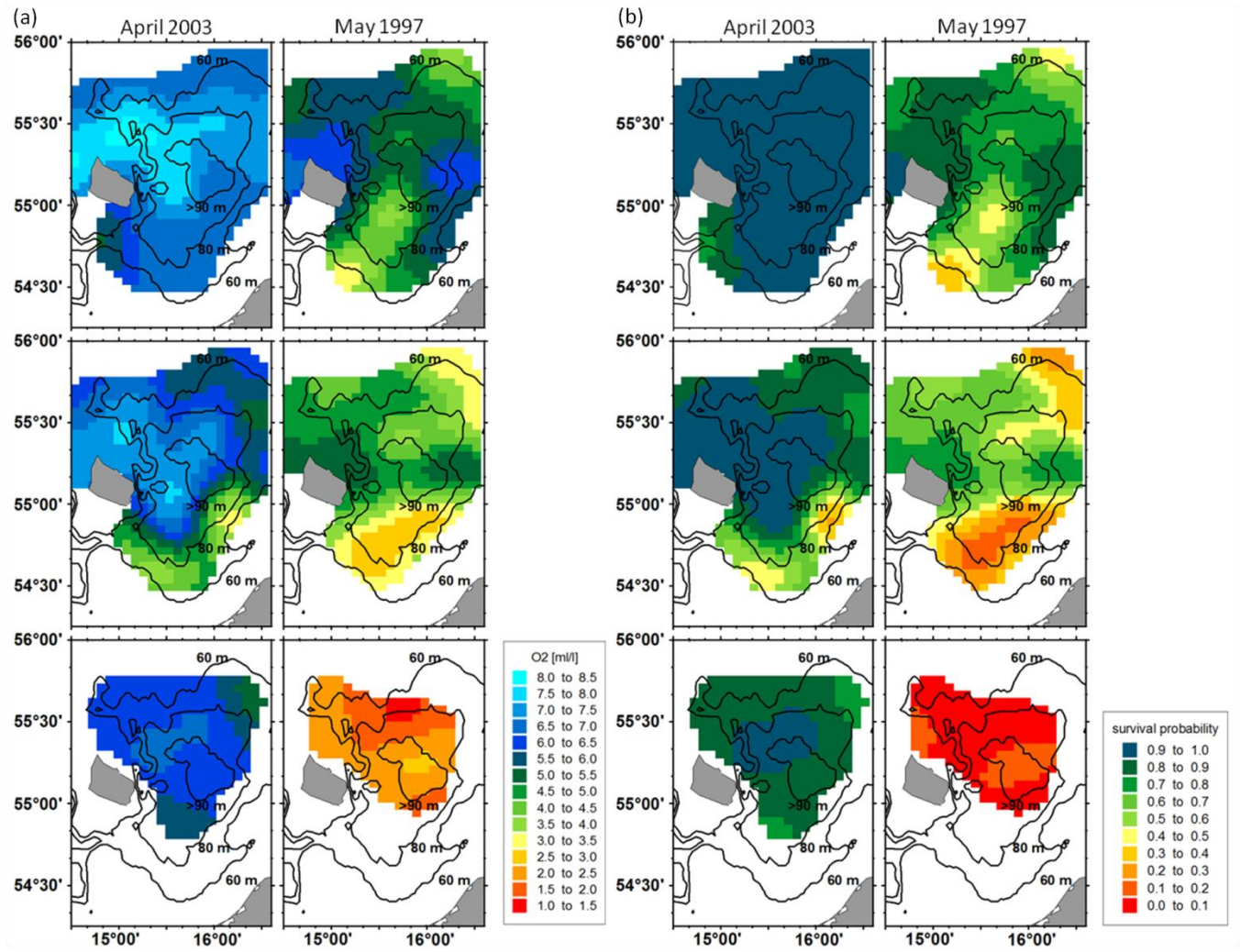

Figure 5: Horizontal maps of oxygen content in ml l−1 (*a*) and Baltic cod oxygen-related egg survival (*b*) for different water density (buoyancy) levels (1009, 1011, 1013 kg m^{-3}) after a major Baltic inflow event in April 2003 and during a stagnation period in May 1997.

Table 3: Monthly mean vertical habitat suitabilities and oxygen-related egg survival probabilities of eastern Baltic cod in the Bornholm Basin (1993–2010).

Month	Neutral egg buoyancy kg m^{-3}]	Area size km^2]	Survival probability	n
April	1009	17469±1299	0.85±0.10	18
May	1009	17253±1249	0.74±0.13	18
July	1009	17313±1517	0.63±0.16	18
April	1011	14472±1807	0.53±0.21	18
May	1011	13131±3217	0.42±0.21	18
July	1011	11779±4652	0.32±0.22	17
April	1013	6321±5039	0.61±0.31	10
May	1013	4368±5324	0.49±0.24	10
July	1013	8886±3219	0.43±0.15	4

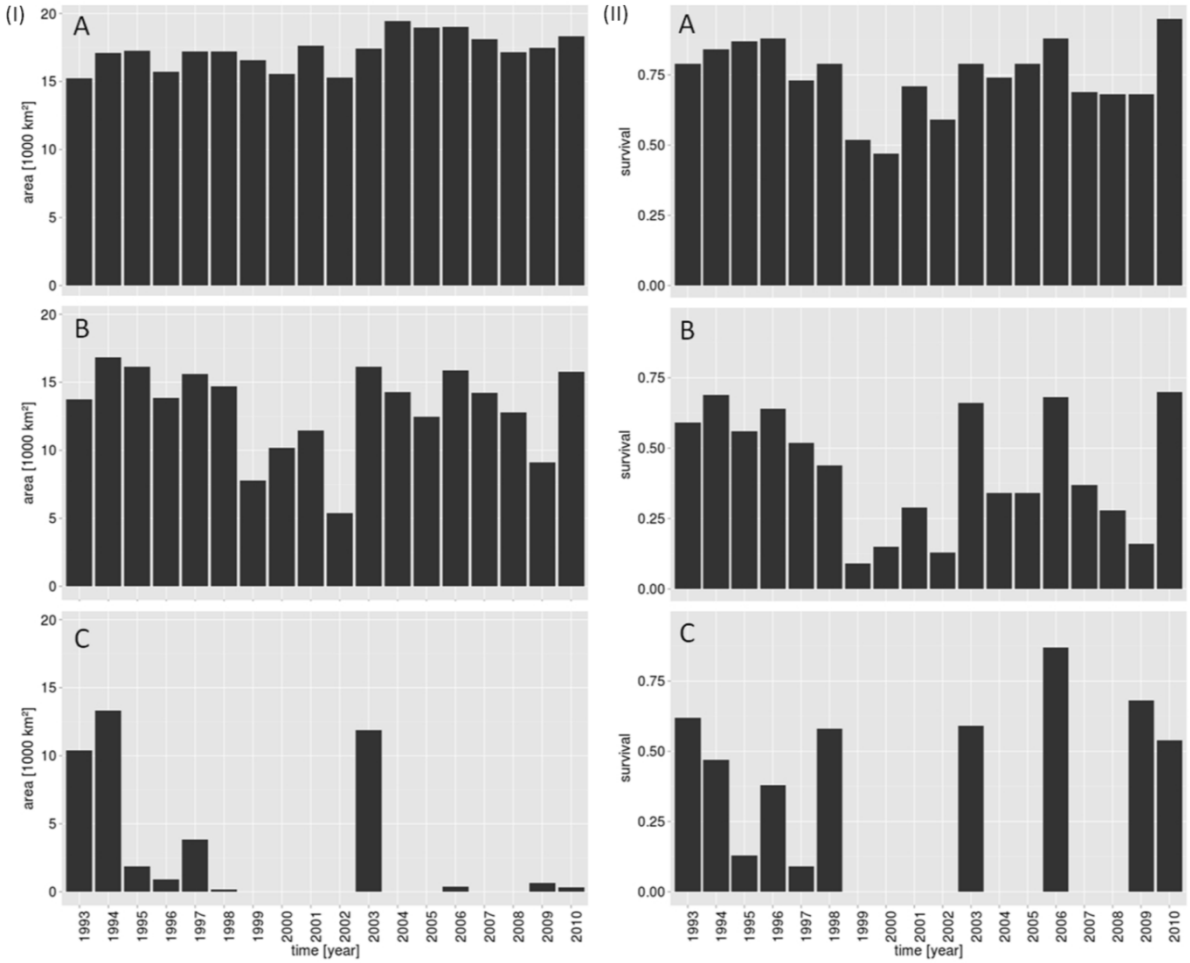

Figure 6: Time series of spawning area extensions in km2 (I) and corresponding Baltic cod oxygen-related egg survival (II) for different water density (buoyancy) levels: (A) 1009, (B) 1011, (C) 1013 kg m^{-3}.

Fig. 6 illustrates the time series of the suitable spawning habitat extension and the oxygen-related cod egg survival probability in spring from 1993 to 2010 for different egg buoyancy levels. For eggs spawned by old, large females the habitat extent was relatively constant ranging from 15000 to 20000 km^2 over the entire time series. In contrast, for eggs of medium aged females, the available habitat was more variable with maximum values of 18000 km^2 during the beginning of the 1990s and mean levels of about 12000 km^2 during the late 2000s. Habitat suitability for this female age category strongly decreased between 1999 and 2002. Finally, habitats for eggs of young spawning females (1013 kg m^{-3}) were to a larger extent only available after the Major Baltic Inflows in 1993 and 1994 (10000 – 15000 km^2), with minor or no suitable habitat availability over the remaining time series.

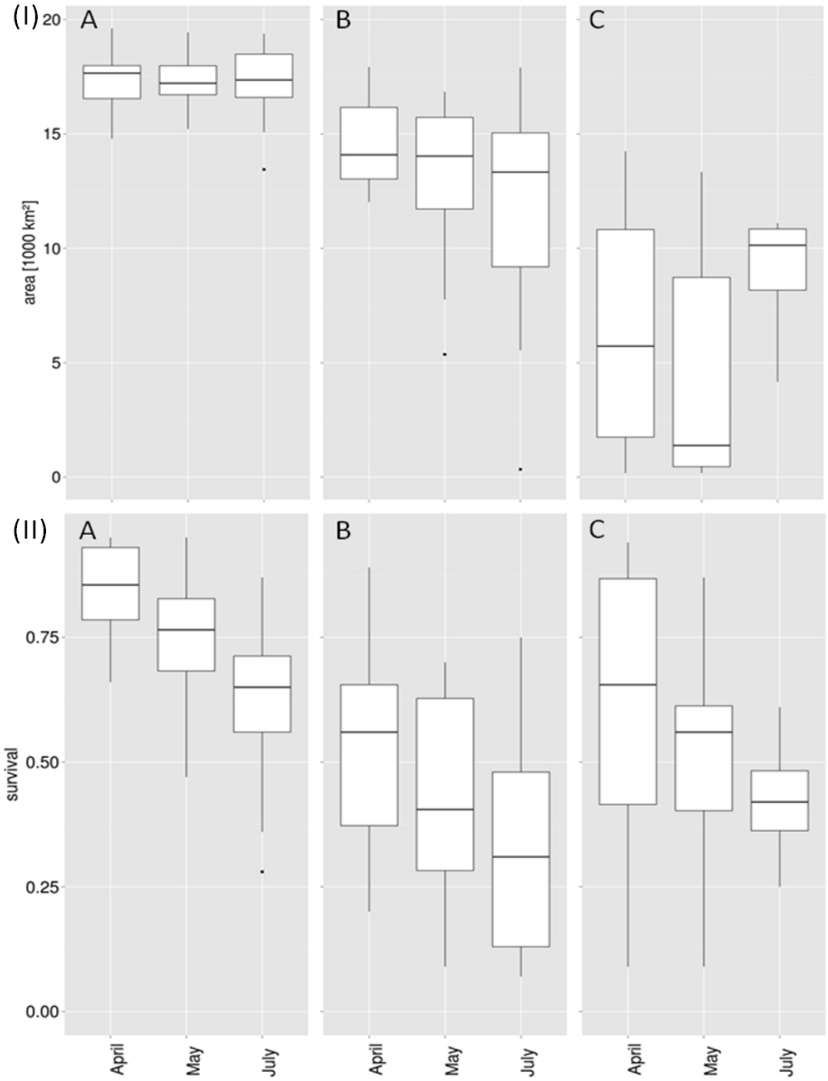

Figure 7: Seasonal differences of spawning area extensions in km2 (I) and corresponding Baltic cod oxygen-related egg survival (II) for different water density (buoyancy) levels: (A) 1009, (B) 1011, (C) 1013 kg m^{-3}.

The oxygen-related cod egg survival probability time series yielded a higher degree of inter-annual variability compared to the corresponding habitat suitabilities. Within the suitable spawning area survival probability of eggs produced by the oldest females varied between 0.5 and 1.0, while for the eggs of the mid-age and young females survival was highly variable (0.1 – 0.7). Highest values occurred during periods following Major Baltic Inflows (1993, 1994 and 2003). Only these inflow events allowed the youngest cod to successfully contribute to reproduction. During these periods the magnitude of their egg survival probability is similar to that observed for the mid-aged spawners.

Seasonal differences in the cod spawning environment (Fig. 7) indicated a substantial decrease of oxygen-related egg survival probability from April to July in all female age categories. This was due to oxygen depletion during the spawning season. In contrast, such a seasonal decrease in spawning habitat extension was only found for mid-aged and young spawning cod, while the habitat for large spawning fish remains almost constant throughout the spawning season. The calculated increase in habitat extension for the young

spawning females at the end of the spawning period is insignificant (n=4; Fig. 7) and is mainly due to inflowing warm and oxygen-rich water masses during summer months in the early 2000s.

The resulting stock-recruitment curve when using eSSB is steeper at low stock sizes and shows a more pronounced density dependence at high stock sizes (Fig. 8). The Ricker-model using eSSB results in a better fit (r^2=0.39) as compared to the standard Ricker-model (r^2=0.28) when inspecting the linearized model. All parameters are highly significant.

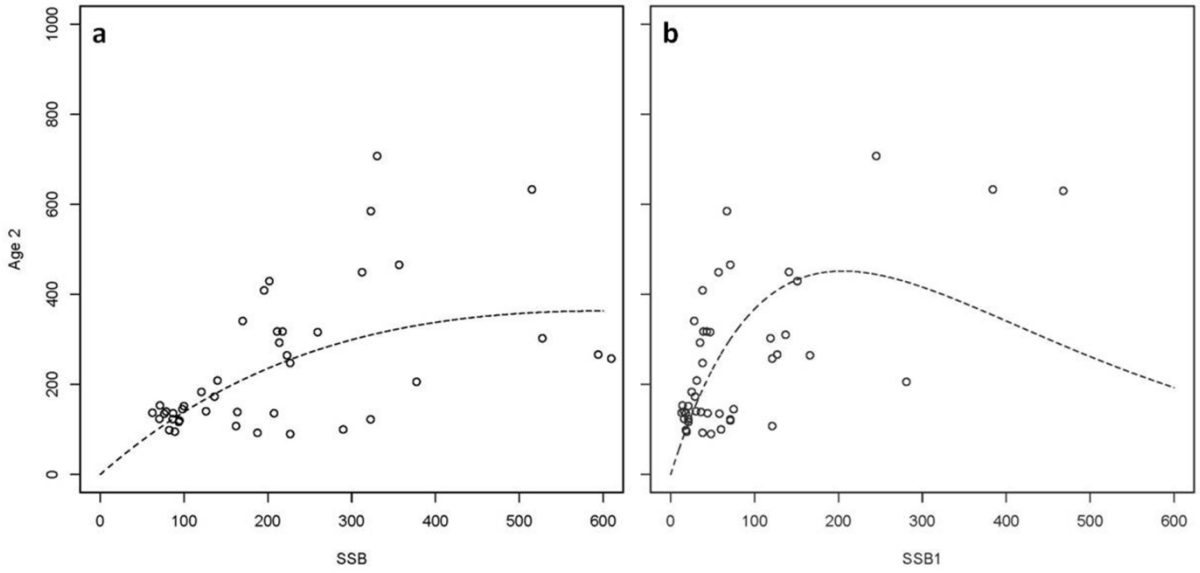

Figure 8: Stock recruitment functions for traditional SSB estimates (*a*) and eSSB, taking into account age-specific egg survival under variable hydrographic conditions (*b*).

Discussion

The novel concept of the effective spawning stock biomass (eSSB) indicator introduced here, and its improved performance relative to traditional SSB as indicator of recruitment, underscored that indices including environmental information can improve biological forecasts and will thus benefit resource management decisions. These benefits may be particularly pronounced in the environmentally challenging conditions of hypoxic area ecosystem (e.g. Baltic and Black Seas), but also mirror the recent broader discussion regarding benefits of ecosystem based vs. single species approaches in fisheries management [36].

The results of our study highlighted the presence of spatio-temporal dynamics in the Eastern Baltic cod spawning habitat extension as well as spawning habitat quality in terms of environmentally driven egg survival. These findings underscore the potential role of environmental conditions for the recruitment success of this stock. Similar conclusions were already obtained previously by [37] based on the single station derived reproduction volume concept as a simple indicators describing an overall integrated measure of spatially varying process information [35]. However, importantly, in contrast to this previous approach, we are now able to disentangle the interactions between spawning stock-related reproductive effort and hydrographic parameters in causing variable recruitment. This

approach is “custom made” for the Baltic. It may also be applicable in the Black Sea, which is comparable in physical settings and ecosystem structure. Here, as in the Baltic Sea, the water column is strongly stratified as salinity increases with depth and the deep water is hypoxic/suboxic/anoxic. Fish eggs are semi-/meso-pelagically distributed [5] as in the Baltic Sea. In contrast the present concept is not applicable to management of fish stocks in the large OMZs of the Atlantic and Pacific oceans, because the physical setting and ecosystem structure of these OMZs differ from that of the Baltic Sea. Here, salinity decreases with depth and, hence, semi-meso-pelagic spawning behavior is not evident, and the vertical distribution of eggs is completely different with no steady-state vertical distributions of semi/meso-pelagic eggs in these regions [38-41].

By considering the direct link between Baltic cod female age, egg buoyancy and egg survival, our results revealed large changes in the horizontal extent of the suitable female age-dependent spawning habitat and the oxygen-dependent egg survival probability between a period following a Baltic inflow event and a stagnation situation. Stagnation periods in the Baltic have long been recognized as potential threat to cod recruitment [42, 43]. Here, we extended these findings by showing that the more buoyant eggs of large females retain a relatively large suitable habitat and survival probability even during a stagnation period, whereas eggs of medium and small females faced strongly reduced habitat and survival probability. The difference of the combined effect of habitat suitability and potential egg survival was about 2-fold between eggs of large and small females after an inflow event, but much larger during stagnation (~ 35-fold).

Including these considerations in the novel indicator eSSB improved the explained variability in recruitment to 39 %, relative to 28% explained by SSB, i.e., performance of “traditional” SSB was improved by more than $1/3^{rd}$. This stressed the biological relevance of the added parameters and the potential usefulness for fisheries management. At the same time, even after including the spawner-age effect, remaining variability (61% relative to 72% unexplained by traditional SSB) in stock-recruitment was still large.

This was probably due to a number of other processes which have been implicated in cod recruitment success, including varying egg predation by sprat and herring [44, 45], maturity [46] and fertilization success [47, 48]. Moreover, during the larval stage, survival may be critically affected by reduced suitable prey abundance [49] and by variable larval drift [50, 51]. Furthermore, as obtained from [23], the inverse relationship between egg diameter and neutral buoyancy levels lacks a considerable amount of explained variability (r^2 = 0.49). This implies that other factors potentially contribute to variations in egg buoyancy. Improved egg buoyancy values could be obtained if the ratio of chorion volume/egg volume of individual eggs is explicitly known [38, 39], i.e. the water content in the yolk (hydrolyzation of the proteins) could vary and influences egg buoyancy. However, compared to the experimentally-derived relationship between egg diameter and buoyancy, the field-based relationship revealed a much higher level of explained variability. Furthermore, individual females produce eggs of different diameters (i.e. buoyancies) within the spawning batch of cod [23, 24], with in general a higher survival potential of the early batches compared to the later ones. Incorporating an average decrease in egg size with batch number and the expected decrease in buoyancy would lower egg

survival estimates over the spawning season even further, but the magnitude of this effect is difficult to quantify. For this reason we calculated simplified egg buoyancy levels (averages over all spawning batches) for each female age-class based on experimental studies [23]. A comprehensive field-based validation is presently still missing, as detailed information on the above mentioned factors are lacking and only limited data sets have been analysed so far [52, 53].

Our results directly indicate the importance of age-class specific reproductive effort in relation to environmentally-based egg survival. Because of strong inter- and intra-annual variations of the central Baltic environment, the Eastern Baltic cod stock is a perfect example for a direct link between female size (age), egg survival potential and recruitment. Any processes that further change the size/age structure of a stock towards smaller size, such as fisheries induced evolution towards for example earlier maturity [54, 55] would exacerbate the reduction of eSSB relative to the total population.

Furthermore, the results emphasize the importance of an age-structured and sex specific abundance index for the Baltic cod stock, similar to ideas suggested for the evaluation of Good Environmental Status within the European Marine Strategy Framework Directive [56-58]. Under the current exploitation regime of eastern Baltic cod, the fish population structure is highly biased towards smaller size and age classes, i.e. “big fat female fish” are rare, but might form (if present) an ecological insurance against increasing hypoxic area extensions. This supports the idea of the “importance of leaving the big ones” [59], and call for the additional inclusion of e.g. a ‘large fish indicator’ [60] in the current stock assessment and management.

Specifically, we propose to use the percentage of old, large females in the stock to be used as a measure of stock resilience to unfavorable environmental conditions. Our results also indicate an effect of stock structure on economic performance of the stock. The same stock biomass comprised of smaller individuals will produce less and more variable recruitment as compared to a stock made up of larger fish. This unfavorable age-structure has to be paid for in terms of lower sustainable harvest, and a risk premium, quantifying the costs of increased cod biomass variability [61, 62].

The key assumptions underlying this paper are that large, older females on average produce larger, more buoyant eggs compared to smaller less buoyant eggs spawned by smaller, younger females [23], and that there is a strong negative correlation of egg diameter with neutral egg buoyancy. In addition, there are reasonable indications that the feeding conditions for adult Eastern Baltic cod might have changed during the most recent decade [63, 64]. Future work repeating laboratory experiments to assess potential changes in female-age dependent egg production and in the egg size relationship and to validate our findings under the present feeding regime would be useful. Other planned future activities include the analysis of female-age dependent egg size/buoyancy relationships in combination with hydrographic data and spatial cod egg distributions to provide information on the availability, accessibility and vulnerability of the different adult female cod age (size) categories in relation to fishing activities during spawning periods. For longer time periods a lack of data exists to entirely resolve the environmental conditions for the major spawning season. To overcome this problem, future applications of our

method will benefit from a new hydrodynamic model version for the Baltic Sea, which will be able to successfully simulate both, oxygen consumption and oxygen replenishment of pelagic as well as benthic zones [65].

Spatial planning based on high quality habitat information of the key species in focus is required (e.g. [66]). Here the temporal dynamics of the ecosystem components influencing the life cycle of key species must be captured in the assessment of habitat suitability and extension and must be taken into consideration when applied in relation to management. Furthermore, long- to medium-term fluctuations of habitats caused e.g. by climate change needs a regularly updated assessment of habitat characteristics to ensure that they reflect the ecosystem under management. Baltic cod egg buoyancy level structured spawning habitat extension and quality could be quantitatively considered as an *essential fish habitat* (EFH) defined as *those waters and substrates necessary to fish for spawning, breeding, feeding, or growth to maturity* according to the US Magnuson-Stevens Act [67].

Because hypoxic area extension in the Baltic Sea is expected to increase, expected habitat losses (e.g. size of spawning grounds) of ecologically and economically important fish species should in future be considered for management decisions regulating fishing pressure as well as harvest rates. Results obtained from IPCC future modeling scenarios show increasing oxygen concentrations in the large OMZs of the Atlantic and Pacific oceans, but predicted a decrease in higher latitudes including the Baltic Sea [8], as the predicted increase in temperature leads to a general decrease in the oxygen solubility of sea water [68, 52].

Advanced and effective ecological indicators (e.g. basin-wide integrated egg survival probability instead of the single station-based reproduction volume of Baltic cod) should have in focus the requirements of EU Marine Strategy Framework Directive indicators, and will contribute to commercial fish stocks within safe biological limits as well as exhibiting a population age and size distribution that is indicative of a healthy stock. As fishery stock assessment and projection tools improved within the last years, it has become easier to incorporate environmental and ecological data into population dynamic models [69] and stock management frameworks.

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Appendices

Appendix 1: The horizontal interpolation technique uses a spatial isotropic Gaussian covariance function of measurements:

$$f(r) = \sigma^2 \exp(-r^2/R^2) \quad (1)$$

with R being the autocorrelation scale parameter and σ the variance and r the distance between data points. R was determined from the fit of this covariance function to the raw covariances of the field observations.

Appendix 2: The results are based on a modeled egg survival function obtained from experimental data [28], not on direct field observations:

$$y_o = 100\left(1-\left(\left(1 - e-\left(0.71x\right)\right)11.63\right)\right), \quad (2)$$

where y_o is the oxygen-dependent survival probability before hatch and x is the oxygen content in ml l^{-1}. Ambient oxygen contents were obtained from our hydrographic database. The function ($r^2 = 0.94$) describes a sigmoid curve with almost total mortality at 2 ml l^{-1} oxygen content, ~50% mortality at 4 ml l^{-1}, and <10% mortality at 7 ml l^{-1}. Generally, oxygen-dependent survival at egg buoyancy levels was calculated with respect to the above mentioned threshold levels in temperature, salinity and oxygen concentration.

Appendix 3: Age-specific weighting factors for eSSB calculation were applied as follows:

$$\text{SSB} = \sum_{s=1}^{8} \gamma_s w_s x_{st}$$

$$\text{eSSB} = \sum_{s=1}^{8} \sigma_s \gamma_s w_s x_{st} \quad (3)$$

where x_{st} are the stock numbers at age s in year t, w_s is weight at age, γ_s maturity at age and σ_s is the age-specific survival factor (age-specific recruitment weighting factor, see Table 2). Data on stock numbers, weight in the stock, and maturity were taken from [8]. In order to assess the usefulness and validity of this new measure we then calculated the amount of variability in recruitment explained by "normal" SSB and by the eSSB. to assess the usefulness and validity of this new measure.

We tested whether the use of the newly-compiled eSSB time-series would improve the fit of a traditional Ricker-type stock-recruitment model, using data from the most recent accepted stock assessment in 2013 [8].

Nonetheless, we first tested which stock-recruitment function yielded the best fit for the traditional SSB estimates. The Ricker-type model fitted the data best, however, being only slightly better than the Beverton-Holt or the smoothed hockey stick model. Therefore, we concentrated on the Ricker model and tested whether the use of the newly-compiled eSSB time-series would improve the fit:

$$\log(R_t) - \log(\text{SSB}_t) = \log(\varphi_1) - \varphi_2 \text{SSB}_t \quad (3a)$$

vs.

$$\log(R_t) - \log(\text{eSSB}_t) = \log(\varphi_1) - \varphi_2 \text{eSSB}_t \quad (3b)$$

References (Chapter1)

1.Stramma L, Johnson GC, Sprintall J, Mohrholz V. 2008 Expanding oxygen-minimum zones in tropical oceans. *Science.* **320**, 655-658.

2.Diaz RJ, Rosenberg R. 2008 Spreading dead zones and consequences for marine ecosystems. *Science* **321**, 926-929.

3.Randell DJ. 1970 Fish Physiology. The Nervous System, Circulation, and Respiration. *Academic.* 253-292.

4.Stramma L, Prince ED, Schmidtko S, Luo J, Hoolihan JP, Visbeck M, Wallace DWR, Brandt P, Kortzinger A. 2012 Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nature Clim. Change.* **2**, 33-37

5. MacKenzie BR, Mariani P. 2012. Spawning of bluefin tuna in the Black Sea: historical evidence, environmental constraints and population plasticity. PLoS ONE 7(7): e39998. 18 p.

6.Ekau W, Auel H, Portner H-O, Gilbert D. 2010 Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosciences* **7**, 1669-1699.

7.Keeling RF, Körtzinger A, Gruber N. 2010 Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* **2**, 199-229.

8.Hoegh-Guldberg O, Cai R, Poloczanska ES, Brewer PG, Sundby S, Hilmi K, Fabry VJ, and S. Jung S. 2014 The Ocean. In: Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1655-1731.

9.Dutil JD, Brander K. 2003 Comparing productivity of North Atlantic cod (Gadus morhua) stocks and limits to growth production. *Fish. Oceanogr.* **12(4-5)**: 502-512

10.ICES. 2013 Report of the Baltic Fisheries Assessment Working Group (WGBFAS). ICES Headquarters, 10-17 April 2013. ICES CM 2013/ACC

11.Kullenberg G, Jacobsen TS. 1988 The Baltic Sea: an outline of it's physical oceanography. *Mar. Pol. Bull*. **12(6)**, 183-186.

12.Møller JS, Hansen IS. 1994 Hydrographic processes and changes in the Baltic Sea. *Dana*. **10**, 87-104.

13.Matthäus W, Franck H. 1992 Characteristics of Major Baltic inflows - a statistical analysis. *Cont. Shelf Res.* **12**, 1375-1400.

14.Carstensen J, Andersen JH, Gustafsson BG, Conley DJ. 2014 Deoxygenation of the Baltic Sea during the last century. *Proc. Nat. Acad. Sci.* **111**, 5628-5633.

15.Nissling A, Valin L. 1996 The ability of Baltic cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. *J. Fish Biol.* **48**, 217-227.

16. Nissling A, Kryvi H, Vallin L. 1994 Variation in egg buoyancy of Baltic cod (*Gadus morhua*) and its implications for egg survival in prevailing conditions in the Baltic Sea. *Mar. Ecol. Prog. Ser.* **110**, 67-74.

17.Wieland K, Waller U, Schnack D. 1994 Development of Baltic cod eggs at different levels of temperature and oxygen content. *Dana* **10**, 163-177.

18.Petereit C, Hinrichsen HH, Franke A, Köster FW. 2014 Floating along buoyancy levels: dispersal and survival in western Baltic fish eggs. *Prog. Oceanogr.* **122**, 131-152.

19.Nissling A, Westin L, Hjerne O. 2002 Reproductive success in relation to salinity for three flatfish species, dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), and flounder (*Pleuronectes flesus*), in the brackish water Baltic Sea. *ICES J. Mar. Sci.* **59(1)**, 93-108.

20.Kjesbu OS, Kryvi H, Norberg B. 1996 Oocyte size and structure in relation to blood plasma steroid hormones in individually monitored, spawning Atlantic cod. *J. Fish Biol.* **49(6)**, 1197-1215.

21.Trippel EA. 1998 Egg size and viability and seasonal offspring production of young Atlantic cod. *Trans. American Fish. Soc. 127(3)*, 339-359.

22.Nissling A, Westin L. 1991 Egg buoyancy of Baltic cod (*Gadus morhua*) and its implications for cod stock fluctuations in the Baltic. *Mar. Biol.* **111**, 33-35.

23.Vallin L, Nissling A. 2000 Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua* - Implications for stock structure effects on recruitment. *Fish. Res.* **49**, 21-37.

24.Möllmann C, Lindegren M, Blenckner T, Bergström L, Diekmann R, Flinkman J, Müller-Karulis B, Neuenfeldt S, Schmidt JO, Tomczak M, Voss R, Gårdmark A. 2014 Implementing ecosystem-based management from single-species to integrated ecosystem assessment and advice for Baltic Sea fish stocks. *ICES J. Mar. Sci.* **71**, 1187-1197.

25.Möllmann C, Diekmann R, Müller-Karulis B, Kornilovs G, Plikshs M, Axe P. 2009 Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: A discontinuous regime shift in the central Baltic Sea. *Global Change Biology*. **15(6)**, 1377-1393.

26.Diekmann R, Möllmann, C (Eds). 2010 Integrated ecosystem assessments of seven Baltic Sea areas. *ICES Cooperative Research Report*. **302**, 90 pp.

27.Lindegren M, Diekmann R, Möllmann C. 2010 Regime shifts, resilience and recovery of a cod stock. *Mar. Ecol. Prog. Ser.* **402**, 239–253.

28.Lindegren M, Blenckner T, Stenseth NC. 2012 Nutrient reduc- tion and climate change cause a potential shift from pelagic to benthic pathways in a eutrophic marine ecosystem. *Global Change Biology* **18**, 3491–3503.

29.Gårdmark A, Nielsen A, Floeter J, Möllmann C. 2011 Depleted marine fish stocks and ecosystem-based management: on the road to recovery, we need to be precautionary. *ICES J. Mar. Sci.* **68**, 212–220.

30.Wieland K. 1995. Einfluss der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (Gadus morhua callarias) im Bornholm Becken, südliche zentrale Ostsee. Berichte aus dem Institut für Meereskunde Kiel, 266 pp.

31.MacKenzie BR, Hinrichsen HH, Plikshs M, Wieland K, Zezera AS. 2000 Quantifying environmental heterogenity: habitat size necessary for successful development of cod Gadus morhua eggs in the Baltic Sea. Mar. Ecol. Prog. Ser.193, 143 – 156.

32.Bretherton FP, Davis RE, Fandry CB. 1976 A technique for objective analysis and design of oceanographic experiments applied to MODE-73. *Deep-Sea Res*. **23**, 559-582.

33.Uzars D, Plikshs M. 2000 Cod (*Gadus morhua* L.) cannibalism in the central Baltic: Interannual variability and influence of recruit abundance and distribution. *ICES J. Mar. Sci.* **57(2)**, 324-329.

34.Hüssy K, St.John M, Boettcher U. 1997 Food resource utilization by juvenile baltic cod gadus morhua: A mechanism potentially influencing recruitment success at the demersal juvenile stage? *Mar. Ecol. Prog. Ser.* **155**, 199-208.

35.Köster FW, Möllmann C, Hinrichsen HH, Wieland K, Tomkiewicz J, Kraus G, Voss R, Makarchouk A, MacKenzie BR, St.John MA, Schnack D, Rohlf N, Linkowski T, Beyer JE (2005) Baltic cod recruitment – the impact of climate variability on key processes. *ICES J. Mar. Sci.* **62**, 1408-1425.

36.Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK, Pope J, Sainsbury KJ. 2004 Ecosystem-Based Fishery Management. *Science*. **305**, 346-347

37.Hinrichsen HH, Voss R, Wieland K, Köster F, Andersen KH, Margonski P. 2007 Spatial and temporal heterogeneity of the cod spawning environment in the Bornholm Basin, Baltic Sea. *Mar. Ecol. Prog. Ser.* **345**, 245–254.

38.Jung KM, Folkvord A, Kjesbu OS, Sundby S. 2014 Experimental parameterisation of principal physics in buoyancy variations of marine teleost eggs. PLOS One, 9(8): e104089. DOI: 10.1371/journal.pone.0104089

39.Kjesbu, OS, Kryvi H, Sundby S, Solemdal P. 1992 Buoyancy variations in eggs of Atlantic cod (Gadus morhua L.) in relation to chorion thickness and egg size, theory and observations Journal of Fish Biology, 41:581-599.

40.Sundby S, Kristiansen T. 2015 The principles of buoyancy in marine fish eggs and their vertical distributions across the world oceans. *PlosOne,* DOI: 10.137/journal.pone.01388211

41.Sundby S, Boyd A, Hutchings L, O'Toole M, Thorisson K, Thorsen A. 2001 Interaction between Cape hake spawning and the circulation in the Northern Benguela upwelling ecosystem. *S. Afr. J. Mar. Sci,* **23**:317-335.

42.Heikinheimo O. 2008 Average salinity as an index for environmental forcing on cod recruitment in the Baltic Sea. *Bor. Env. Res. 13,* 457-464.

43.Lindegren M, Möllmann C, Nielsen A, Stenseth NC. 2009 Preventing the Collapse of the Baltic Cod Stock through an Ecosystem-based Management approach. *Proc. Natl. Acad. Sci.* USA **106**,14722-14727.

44.Köster FW, Möllmann C. 2000 Trophodynamis control by clupeid predators on recruitment success in Baltic cod? *ICES J. Mar. Sci.* **57**, 310-323.

45.Voss R, Hinrichsen HH, Stepputtis D, Bernreuther M, Huwer B, Neumann V, Schmidt JO. 2011 Egg mortality: Predation and hydrography in the central Baltic. *ICES J. Mar. Sci.* **68(7)**, 1379-1390.

46.Kraus G, Tomkiewicz J, Köster FW. 2002 Egg production of Baltic cod (*Gadus morhua*) in relation to variable sex ratio, maturity, and fecundity. *Can. J. Fish. Aquat. Sci.* **59(12)**, 1908–1920.

47.Trippel EA. 2003 Estimation of male reproductive success of marine fishes. *J.Northwest Atl. Fish. Sci.* **33**, 81-113.

48.Frommel AY, Stiebens V, Clemmesen C, Havenhand J. 2010 Effect of ocean acidification on marine fish sperm (Baltic cod: *Gadus morhua*). *Biogeosciences.* **7(12)**, 3915-3919.

49.Kristiansen T, Vikebo F, Sundby S, Huse G, Fiksen O. 2009 Modeling growth of larval cod (*Gadus morhua*) in large-scale seasonal and latitudinal environmental gradients. *Deep Sea Res. II.* **56(21-22)**, 2001-2011.

50.Voss R, Hinrichsen HH, St.John M. 1999 Variations in the drift of larval cod (*Gadus morhua* L.) in the Baltic Sea: combining field observations and modelling. *Fish. Oceanogr.* **8(3)**, 199-211.

51.Hinrichsen HH, Möllmann C, Voss R, Köster FW, Kornilovs G. 2002a Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. *Can. J. Fish. Aquat. Sci.* **59(12)**,1858-1873.

52.Hinrichsen HH, Huwer B, Makarchouk A, Petereit C, Schaber M, Voss R. 2011 Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (*Gadus morhua*). *ICES J. Mar. Sci.* **68(10)**, 2019 – 2028.

53.Wlodarczyk E, Horbowa K. 1997 Size-specific vertical distribution of Baltic cod (*Gadus morhua* L.) eggs in the Bornholm Basin in 1993 and 1994. *ICES J. Mar. Sci.* **54**, 206-212.

54.Andersen KH, Farnsworth KD, Thygesen UH, Beyer JE. 2007 The evolutionary pressure from fishing on size at maturation of Baltic cod. *Ecol. Mod.* **204**, 246-252.

55.Olsen EM, Heino M, Lilly GR, Morgan MJ, Brattey J, Ernande B, Dieckmann U. 2004 Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**, 932-935.

56.Probst WN, Kloppmann M, Kraus G (2013a) Indicator-based assessment of commercial fish species in the North Sea according to the EU Marine Strategy Framework Directive (MSFD). *ICES J. Mar. Sci.* **70**, 694-706.

57.Probst WN, Stelzenmüller V, Kraus G (2013b) A simulation-approach to assess the size structure of commercially exploited fish populations within the European Marine Strategy Framework Directive. *Ecol. Ind.* **2**4, 621-632.

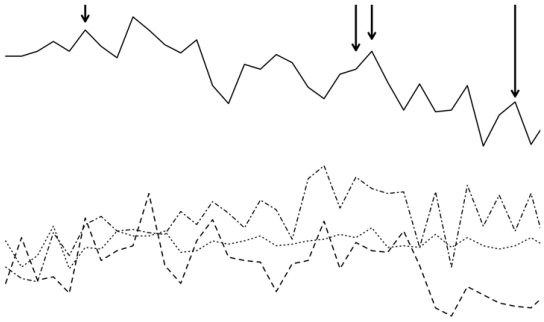
58.EU-COM. 2010 Commission decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters, In: *Commission,* E. (Ed.), 2010/477/EU. European Commission.

59.Birkeland C, Dayton PK. 2005 The importance in fishery management of leaving the big ones. *Trends Ecol. Evol.* **20**:356-358

60.Greenstreet SPR, Rogers SI, Rice JC, Piet GJ, Guirey EJ, Fraser HM, Fryer RJ. 2011 Development of the EcoQO for the North Sea fish community. *ICES J. Mar. Sci.* **68**, 1-11.

61.Kapaun U, Quaas MF. 2013 Does the optimal size of a fish stock increase with environmental uncertainties? *Env. Res. Econ.* **54(2)**, 293-310.
62.Blenckner T, Llope M, Möllmann C, Voss R, Quaas MF, Casini M, Lindegren M, Folke C, Stenseth N, 2015 Climate and fishing steer ecosystem regeneration to uncertain economic futures. *Proc. Royal Society B.* **282**, 2014-2809.
63.Røjbek MC, Jacobsen C, Tomkiewicz J, Stottrup JG. 2012 Linking lipid dynamics with the reproductive cycle in Baltic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **471**, 215-234.
64.Eero M, Vinther M, Haslob H, Huwer B, Casini M, Storr-Paulsen M, Köster FW. 2012 Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. *Cons. Lett.* **5(6)**, 486-492.
65.Lehmann A, Hinrichsen HH, Getzlaff K, Myrberg K. 2014 Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumtion model approach. *J. Mar. Syst.* **134**, 20-28.
66.Pedersen SA, Fock HO, Sell AF. 2009 Mapping fisheries in the German Exclusive Economic Zone with special reference to offshore Natura 2000 sites. *Mar. Pol.* **33**, 571-590.
67.Magnusson-Stevens Act. The Magnusson-Stevens Fishery Conservation and Management Act.
68.Hinrichsen HH, St.John M, Lehmann A, MacKenzie BR, Köster FW. 2002b Resolving the impact of short-term variations in physical processes impacting on the spawning environment of eastern Baltic cod: application of a 3-D hydrodynamic model. *J Mar Syst*. **32**:281-294
69.Aarts G, Poos JJ. 2009 Comprehensive discard reconstruction and abundance estimation using flexible selectivity functions. *ICES J. Mar. Sci.* **66**, 763–771.

Chapter 2



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Spatio-temporal dynamics of cod nursery areas in the Baltic Sea

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Highlights:

- Model output indicates high connectivity between the eastern Baltic cod nursery grounds.
- Variability of spatial juvenile cod habitat has been declining over the last decades.
- Condition of juveniles suggests density-dependence due to hypoxia-related decrease in suitable habitat.
- Baltic cod recruitment indicator: habitat availability for juvenile settlement as a factor for recruitment.

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Abstract

In this study the drift of eastern Baltic cod larvae and juveniles spawned within the historical eastern Baltic cod spawning grounds was investigated by detailed drift model simulations for the years 1971 to 2010, to examine the spatio-temporal dynamics of environmental suitability in the nursery areas of juvenile cod settlement. The results of the long-term model scenario runs, where juvenile cod were treated as simulated passively drifting particles, enabled us to find strong indications for long-term variations of settlement and potentially the reproduction success of the historically important eastern Baltic cod nursery grounds. Only low proportions of juveniles hatched in the Arkona Basin and in the Gotland Basin were able to settle in their respective spawning ground. Ocean

currents were either unfavorable for the juveniles to reach suitable habitats or transported the juveniles to nursery grounds of neighboring subdivisions. Juveniles which hatched in the Bornholm Basin were most widely dispersed and showed the highest settlement probability, while the second highest settlement probability and horizontal dispersal was observed for juveniles originating from the Gdansk Deep. In a long-term perspective, wind-driven transport of larvae/juveniles positively affected the settlement success predominately in the Bornholm Basin and in the Bay of Gdansk. The Bornholm Basin has the potential to contribute on average 54 % and the Bay of Gdansk 11% to the production of juveniles in the Baltic Sea. Furthermore, transport of juveniles surviving to the age of settlement with origin in the Bornholm Basin contributed on average 13 and 11% to the total settlement in the Arkona Basin and in the Gdansk Deep, respectively. The time-series of the simulated occupied juvenile cod habitat in the Bornholm Basin and in the Gdansk Deep showed a similar declining trend as the Fulton's *K* condition factor of demersal 1-group cod, which may confirm the importance of oxygen-dependent habitat availability and its effect on density dependence as a process relevant for recruitment success.

Introduction

Many marine species use different habitats for adult feeding, spawning, larval development, larval and juvenile feeding, and juvenile settlement. Their life histories require connections between these spatially disaggregated locations to close the life cycle (Hay et al., 2001). A key process influencing recruitment success in fish populations is the spatio-temporal variability in egg and larval transport from spawning grounds to suitable nursery areas (e.g. Werner et al.,1996; Heath and Gallego 1998; Hinrichsen et al.,2002; Hinrichsen et al., 2009).

The processes potentially determining dispersal and retention of fish early life stages include the timing and location of spawning, habitat availability, stage of development, temperature-dependent development time, individual buoyancy, diurnal and ontogenetic vertical migration, temperature- and food-dependent growth, starvation mortality, predation mortality and settlement success. Of further importance are physical variables such as e.g. temperature, oxygen concentration, ocean currents and turbulence (e.g. Gallego et al., 2007; Miller et al., 2007), as well as the interaction of those variables with the above mentioned biotic factors.

The spawning stock of eastern Baltic cod has decreased significantly during the past decades, due to the combined effect of climate driven processes (e.g. increase of temperature and decrease in oxygen content) and anthropogenic factors (e.g. high fishing pressure, eutrophication; Eero et al., 2015). High fishing pressure has resulted in a decreasing spawning stock, while unfavourable abiotic environmental conditions have had a negative impact on the survival and development of the early life stages (Hinrichsen et al., 2002; Köster et al., 2005 and 2016; Eero et al., 2015). Successful spawning of eastern Baltic cod is supposed to be limited to water with suitable conditions in terms of salinity (>11 psu), oxygen (>2 ml/l), and temperature (>2 °C) (e.g. Wieland et al., 1994). These factors depend on wind driven saltwater

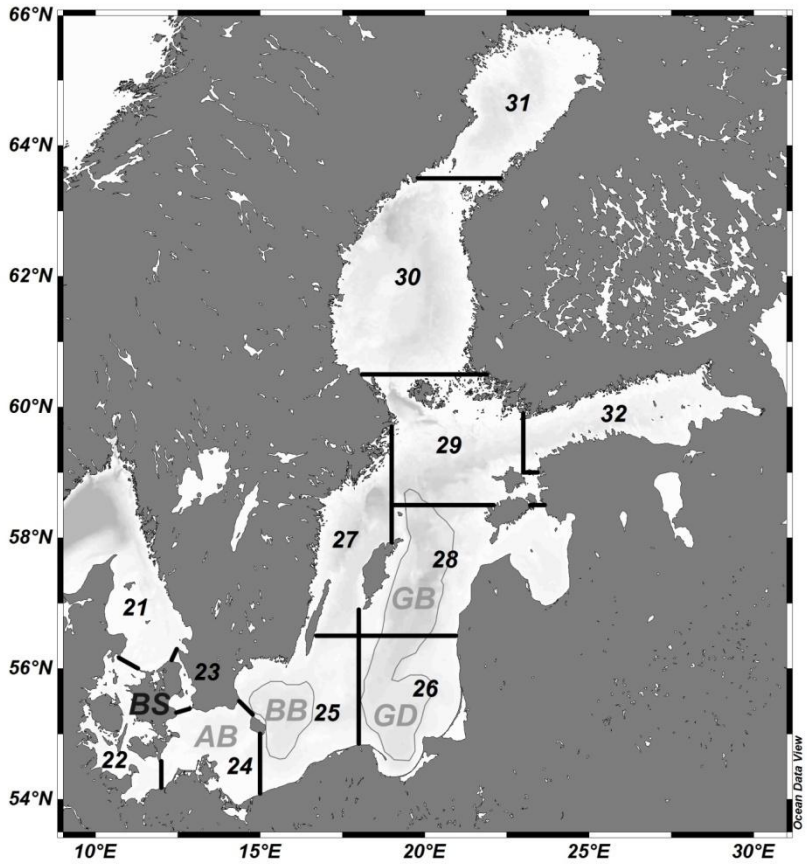

Figure 1: ICES subdivisions in the Baltic Sea and Baltic cod spawning areas: BS – Belt Sea, AB – Arkona Basin, BB – Bornholm Basin, GD – Gdansk Deep, GB – Gotland Basin.

inflows (Hinrichsen et al., 2002), river-runoff and eutrophication (Lehmann et al., 2014). Successful recruitment is also dependent on the abundance of zooplankton and their spatial and temporal overlap with larval cod, and thus indirectly on the consumption of zooplankton by planktivorous fish species, such as sprat and herring, as well as on predation of cod eggs by sprat and herring (Hinrichsen et al., 2002; Köster et al., 2005; Casini et al., 2006). Processes impacting the developmental success of the juvenile stage, both in the demersal and especially in the pelagic phase are not well understood (Bagge et al., 1994). However, without finding a suitable settling habitat in an appropriate time frame, which will allow cod to feed on larger, benthic organisms, juveniles might face starvation and possibly death during their first winter (Hüssy et al., 1997). Sufficient availability of benthic prey items is found in regions with relatively high oxygen concentration at the bottom (Casini et al., 2016). As shown by Hinrichsen et al. (2009), the spatial and temporal variability in oxygen concentration in bottom layers might determine the settling probability of the juveniles, the oxygen-related consumption rate and might concurrently affect their condition by temporal variability of the benthic food supply for the demersal stage (Hinrichsen et al., 2011, Maczassek, 2006).

The occurrence of distinct spawning grounds of eastern Baltic cod and strong variations of the circulation patterns suggests the usage of a hydrodynamic model and Lagrangian particle tracking to study the potential existence of self-sustaining eastern Baltic cod stock components. Drift modelling studies have been used for eastern Baltic cod earlier to investigate the dispersal dynamics of early life stages (Voss et al., 1999; Hinrichsen et al.,

2003), the impact on the survival of larvae (Hinrichsen et al., 2001), and the influence of copepod species composition on the growth and survival of larvae (Hinrichsen et al., 2002). Previous drift modeling studies have also shown that there is considerable connectivity between areas through dispersal of early life stages (Hinrichsen et al., 2009). A spatially and temporally highly-resolved biophysical model of Baltic Sea was also utilized to describe mortalities and survival success of western Baltic cod eggs and yolk-sac larvae (Hinrichsen et al., 2012; Hüssy et al., 2012). Mortality of western Baltic cod eggs (ICES subdivisions 21-24) was mainly caused by sedimentation (bottom contact) and/or lethal temperatures, while oxygen content had virtually no impact on egg survival in the western cod spawning environment owing to the generally high oxygen saturation levels (Petereit et al., 2014). Hence, any modeling effort on this specific topic seems presently not reasonable for western Baltic cod eggs.

One of the major challenges for hydrodynamic modeling of the eastern Baltic Sea has been the simulation of deep water dissolved oxygen distribution with its seasonal and quasi-permanent extended areas of oxygen deficiency. Such a model was successfully constructed by Lehmann et al. (2014). The results of this study, for the first time, allowed the consideration of oxygen content as the major contributor to egg mortality for the eastern Baltic cod stock. However, Hinrichsen et al. (2009) have already used a biophysical modeling approach to analyze the suitability of eastern Baltic cod juvenile settlement. To obtain a proxy for the settlement habitat quality and hence an oxygen-related potential mortality source of eastern Baltic juvenile cod, monthly mean oxygen profiles for ICES subdivisions provided by the ICES oceanographic data base were used, because spatially and temporally highly-resolved hydrodynamic model-based oxygen distributions (Lehmann et al., 2014) were at that time not available.

The objectives of this study are to examine environmentally-related drift and oxygen-related settling probability of eastern Baltic larval and juvenile cod based on new knowledge of spatially and temporally highly resolved oxygen conditions and to estimate the potential for population connectivity between different spawning grounds of eastern Baltic cod by larval drift. Furthermore, oxygen-dependent habitat suitability for juvenile settlement is compared with habitat utilization of successfully settled juvenile cod represented as drifting particles. Finally we compare spatially resolved patterns of these simulated settled juveniles with observed distributions from surveys. To evaluate for applicability of the biophysical model, we present a sensitivity analysis by examining the implications of parameter variation on juvenile settlement probability.

Materials and Methods

Hydrodynamic modeling: The basis of the Lagrangian particle tracking is the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM, Lehmann & Hinrichsen, 2000; Lehmann et al., 2002). At present the horizontal resolution of the coupled sea-ice ocean model is 2.5 km, and in the vertical 60 levels are specified, which means the upper 100 m is resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, Kattegat and Skagerrak. The oxygen conditions in the entire Baltic Sea are described by an oxygen consumption sub-model coupled to BSIOM (Lehmann et al., 2014). A detailed description of the evolution of oxygenated, hypoxic and anoxic areas is particularly required when studying oxygen-related processes such as habitat utilization of spawning fish, survival rates of their eggs, as well as settlement probability of juveniles. Long-term model runs have provided results on oxygen which are in good agreement with hydrographic measurement, i.e. monthly mean ICES data (Fig. SM1) and monthly mean data on the eastern Baltic cod reproduction volume (Lehmann et al., 2014; their figure 6). For the latter a correlation of r=0.71 was obtained. At the western boundary, a simplified North Sea basin is connected to the model domain to represent characteristic North Sea water masses in terms of characteristic temperature and salinity profiles resulting from different forcing conditions. The model is forced by low frequency sea level variations in the North Sea/Skagerrak calculated from the BSI (Baltic Sea Index, Lehmann et al., 2002; Novotny et al., 2006). The coupled sea ice-ocean model is forced by realistic atmospheric conditions taken from the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database (Lars Meuller, pers. comm.) which covers the whole Baltic drainage basin on a regular grid of 1 x 1° with a temporal increment of 3 hours. The database consists of synoptic measurements that were bi-linearly interpolated on the regular grid with a two-dimensional optimum interpolation scheme. This database, which for modeling purposes was further interpolated onto the model grid, includes surface pressure, precipitation, cloudiness, air temperature and water vapour mixing ratio at 2 m height and geostrophic wind. Wind speed and direction at 10 m height were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast (Bumke et al., 1998). BSIOM forcing functions, such as wind stress, radiation and heat fluxes were calculated according to Rudolph and Lehmann (2006). Additionally, river runoff was prescribed from a monthly mean runoff data set (Kronsell and Andersson, 2012). The numerical model BSIOM has been run for the period 1971-2010. This time series was used for the subsequent analysis of juvenile cod habitat suitability and early life stage survival in the Baltic Sea.

Estimation of available Baltic cod juvenile habitat: Simulated three-dimensional oxygen saturation fields were extracted from the hydrodynamic model output in order to generate a database for the calculation of the available eastern juvenile Baltic cod settlement area. For spatial analyses of habitat occupancy percentages of occurrence of suitable habitat (oxygen saturation levels > 60%) on the near bottom layer were calculated for each grid box. Additionally, for each of the larval release dates (years 1971-2010, Julian days 91-261) we have calculated the area sizes in the near-bottom layer in the Arkona Basin, the Bornholm Basin, the Gdansk Deep and the Gotland Basin (ICES SDs 24, 25, 26 and 28 respectively) (Fig. 1) in which oxygen saturation levels > 60% were present.

Particle tracking model and estimation of occupied Baltic cod juvenile habitat: Simulated three-dimensional temperature, salinity, oxygen and velocity fields were extracted (at 3 hour intervals) from the hydrodynamic model in order to develop a database for particle tracking. This data set offers the possibility to derive Lagrangian drift routes from Eulerian flow fields by calculating the advection of "marked" water particles. The three-dimensional trajectories of the simulated drifters were computed using a 4th order Runge-Kutta scheme (Hinrichsen et al., 1997), where larval and juvenile cod were treated as simulated passively drifting particles.

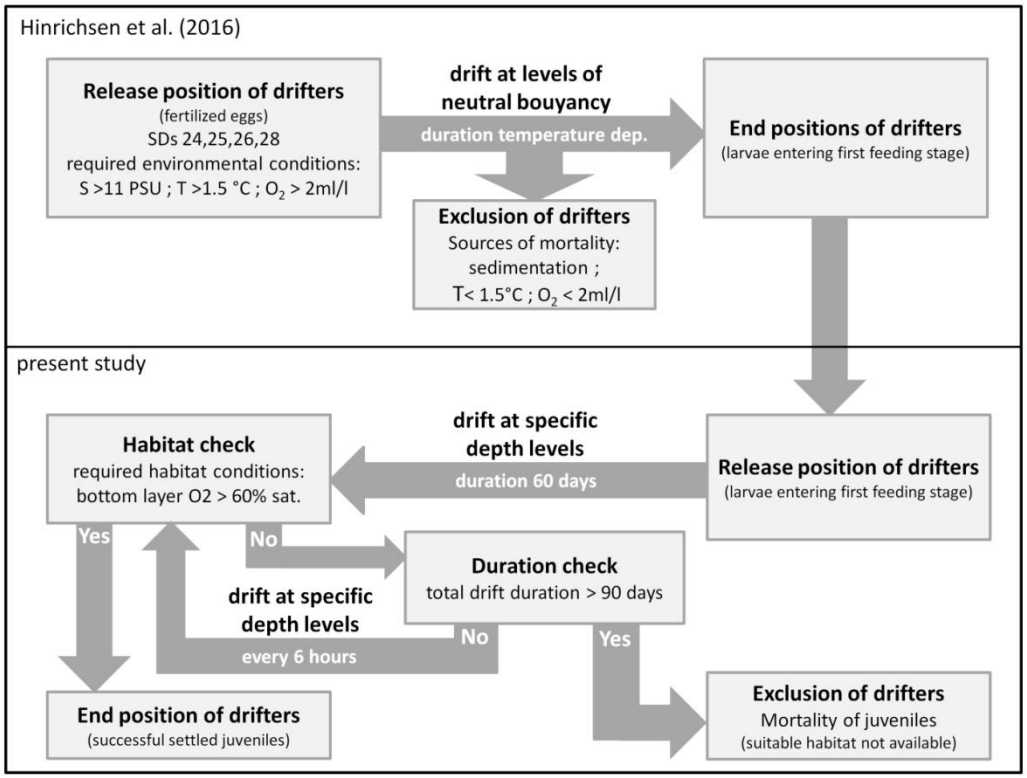

Figure 2: Schematic flow of Baltic cod early life stage drift modeling (this study and Hinrichsen et al., 2016).

Larvae at the developmental first feeding stage were released into the simulated flow fields and tracked through the model domain until settling is required. The drifting particles are released within the historically important Baltic cod spawning grounds (Fig. 1) as first feeding larvae obtained from the long-term spatial distribution (1971-2010) of survivors up to the first feeding yolk sac larval stage. The initial horizontal distribution patterns of this life stage is taken from results obtained from a drift study on eastern Baltic cod eggs performed by Hinrichsen et al., 2016 (their Fig. 9 and Fig. 2, this manuscript), i.e., the amount of drifters released is based on the spatial distribution of survivors in the cod egg study. Hence this is an improvement compared to the modeling approach utilized by Hinrichsen et al. (2009). Drifting particles were released at depths between 25 and 50 m on a regularly spaced grid (2.5 x 2.5 km). The majority of feeding larvae occur after their initial ontogenetic vertical migration in this depth range with weak diel vertical migration behaviour (Grønkjær et al., 1997).

Based on hydrodynamic modeling ambient temperature, salinity and oxygen values were recorded along the whole trajectories. Once a drifting particle reached the settlement age of

about 60 to 90 days (Hüssy et al., 2003), it performed a "habitat check". This above mentioned time range is a simplified approach as detailed knowledge of juvenile behaviour (active horizontal and/or vertical movements) during their search for suitable settlement habitats is not available. Typically, adult cod require a minimum of ~40% oxygen saturation (Chabot and Dutil, 1999), but specific information about oxygen preference or tolerance of eastern Baltic cod juveniles at the stage of settlement is not available. In this study, the environmental threshold level for juvenile settlement was based on recent, preliminary investigations (minimum of 60% oxygen saturation at settlement; Neuenfeldt, pers. comm.). The "habitat check" was performed as follows: after 60 days of drift duration, the drifting particles were stopped every time step to check if the required minimum oxygen saturation level (> 60%) was reached under the assumption that juveniles settle to the bottom when they encounter suitable habitat. Once the required habitat was found, the location of settlement and the corresponding environmental conditions were recorded. In case drifting particles were not able to find sufficient oxygen saturation at the bottom within the upper age limit for settlement of 90 days, the individual particles were not counted as settled juveniles.

Spawning time and spawning areas: The focus of this study is on the eastern Baltic cod's general reproduction potential for the whole spawning season. This stock is known to spawn from February to November, with the main spawning season in April – August with considerable inter-annual variability in peak spawning (Wieland et al., 2000; Bleil et al., 2009). In order to consider seasonal variability in relation to spatial and temporal variations in larval transport, drifting particles were inserted into the modeled flow fields at 10-day intervals. However, to consider any recently observed extension of the main spawning season to later months, the larval release dates covered the period 1st April to 20th September, encompassing the historical as well as the present main spawning period of Eastern Baltic cod (Wieland et al., 2000). The locations of the spawning grounds of the eastern Baltic cod stock (Bornholm Basin, Gdansk Deep, Gotland Basin) were taken from Bagge et al. (1994), while a potential spawning ground of the eastern Baltic cod stock in the Arkona Basin was selected based on already existing information provided by Nissling and Westin (1997).

Field caught juveniles: In order to test the accuracy of model-predicted nursery areas, vertical distribution patterns of drifter destinations were compared with observed distributions of juvenile cod. Information on spatial distribution patterns of eastern Baltic cod juveniles has been collected regularly in the framework of the BITS trawl surveys since 1991. Length frequencies as well as size and weight information of individual fish, with the associated catch position and depth information from these surveys was downloaded from ICES' database of trawl surveys (DATRAS) (http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx). Compared to the drift study analyses, the time-series of these surveys is limited to the years 1991 and onward. Only data of cod < 16 cm from the first quarter of the year were used, which corresponds to 1-group demersal juvenile fish. All depth records were binned to 5 m depth intervals. From the length distributions, the number of juveniles caught by depth interval was divided by the total number of juveniles caught during the survey. Since sampling stations are not uniformly distributed between depths, this frequency was scaled to the number of stations

occurring in each depth stratum in relation to the total number of stations in the survey. Depth distributions were calculated for the Arkona Basin, the Bornholm Basin, the Gdansk Deep and the Gotland Basin separately. Since habitat availability and quality has been suggested as one of the factors affecting adult cod's somatic condition (Eero et al., 2015; Casini et al., 2016), the impact of nursery habitat size on condition was evaluated for each SD separately in the present study. For each individual the Fulton's body condition index was calculated as $K = 100 \cdot \text{weight (g)} \cdot \text{length (cm)}^{-3}$. This index is an indicator of the somatic condition of demersal juvenile cod. Fulton's *K* condition factor of juvenile cod was calculated to obtain an indication of reduced growth due to density dependent-processes as the result of a decrease in the availability of juvenile habitat. In total, annual mean values of *K* (± 1 sd) were calculated for 892, 1930, 1087 and 798 juveniles sampled during trawl surveys in the Arkona Basin, the Bornholm Basin, the Gdansk Deep and the Gotland Basin in the 1st quarter of the years from 1991 to 2010. Data of Fulton's *K* index were smoothed using Loess smoothing with a span (degree of smoothing) of 0.2 and second degree polynomials and represented as means with 95% confidence interval bands (R Development Core Team, 2009).

Comparison of drifter end positions with spatial distribution of juvenile cod: See Supplementary Material.

Sensitivity analyses on the biophysical model: See Supplementary Material

Results

Spatially disaggregated patterns of available juvenile cod habitat: Fig. 3 shows the mean spatial frequency distribution of available juvenile cod habitat (oxygen saturation level > 60% at the bottom) for 1971-2010. The bottom oxygen conditions frequently were found to be above the 60% oxygen threshold level in the shallow and slope areas of all ICES subdivisions as well as in the deep water areas of the Arkona Basin, while in the deep water areas (below 60 m depth) of the Bornholm Basin, the Gdansk Deep and the Gotland Basin oxygen saturation was almost constantly below 60%.

Time series of total areal extent of available habitat for the different ICES subdivisions are displayed in Fig. 4. Generally, the highest available habitat occurred in the Bornholm Basin (SD25). On average, the total habitat extent was lower in the Arkona Basin, the Gdansk Deep and the Gotland Basin (SDs 24, 26 and 28, respectively). For almost the entire time series the

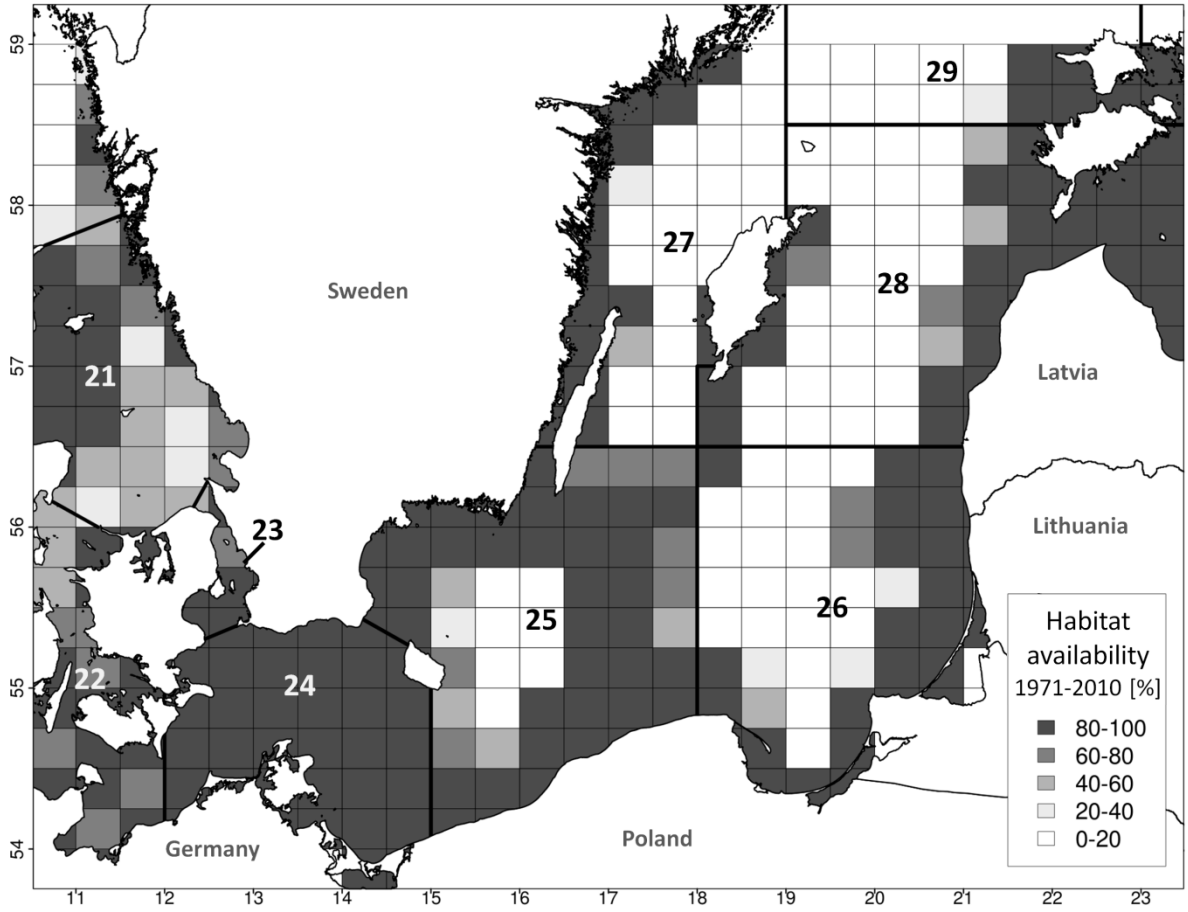

Figure 3: Frequency of available juvenile cod habitat (oxygen saturation level >60%) for the period 1971–2010.

whole bottom area in the Arkona Basin was suitable for juvenile cod settlement (~30000 km^2). On average, available habitat in the Bornholm Basin is higher (~45000 km^2), whereas in the Gdansk Deep falls in between (~37000 km^2). The habitat sizes in the Bornholm Basin and in the Gdansk Deep were highly variable with a weak declining trend starting at the end of the 1980s. For the whole time series available habitat in the Gotland Basin is on a high almost constant level (~42000 km^2). Assessment of the long-term development of juvenile eastern Baltic cod habitat size for different ICES subdivisions is summarized in Table 1.

Spatially disaggregated patterns of occupied juvenile habitat: The long-term development of occupied juvenile cod habitat (Fig. 5) mirrors that of the available juvenile cod habitat. However, for all ICES subdivisions the areas where the juvenile drifters finally settled were 10 to 20% smaller in size compared to the available habitat. However, the long-term development of the area of occupied juvenile habitat in the Bornholm Basin and in the Gdansk Deep reveals two fold higher annual decreases compared to the available habitat (Table 1), while the long-term trend of the occupied habitat in the Gotland Basin slightly increased.

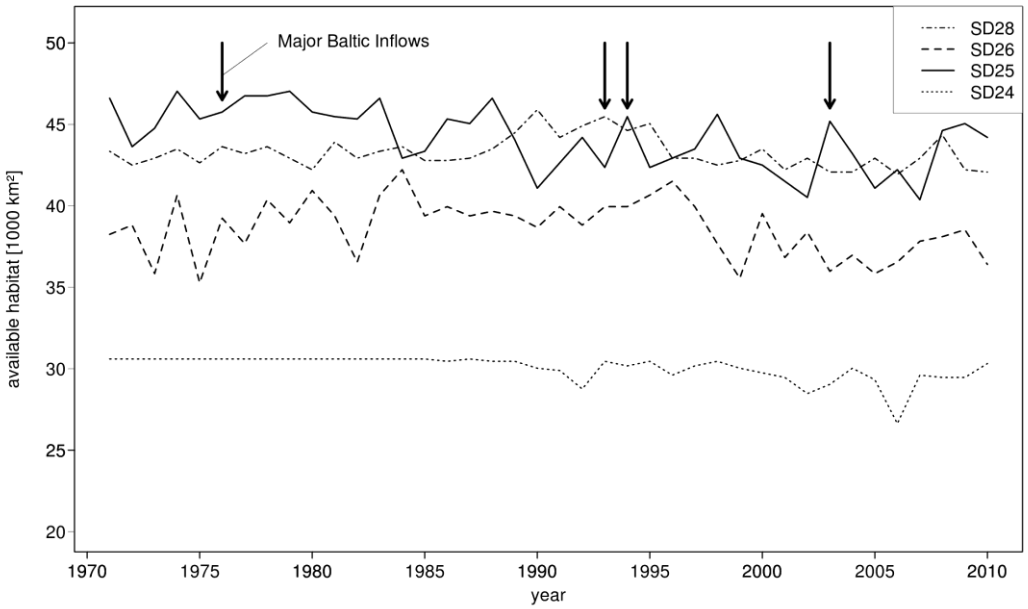

Figure 4: Annually averaged available juvenile cod habitat [1000 km^2] in the Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28).

Table 1: Mean annual change [km^2] of juvenile cod settlement areas in ICES subdivisions.

	SD24	SD25	SD26	SD28
Change of available habitat	-40	-90	-40	-12
Change of occupied habitat	-12	-200	-100	70

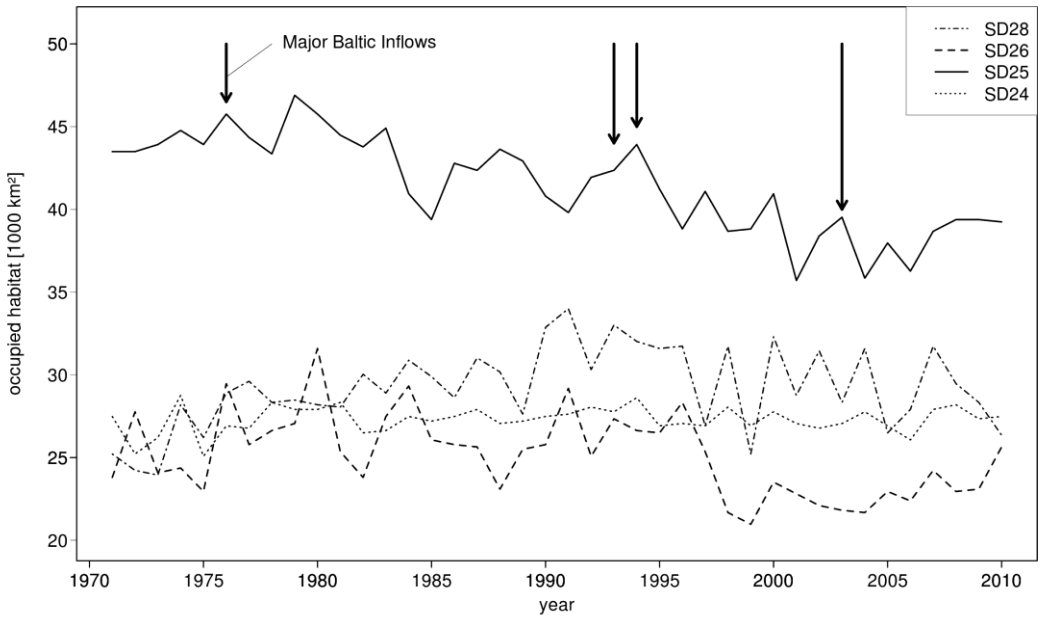

Figure 5: Annually averaged occupied juvenile cod habitat [1000 km^2] in the Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28).

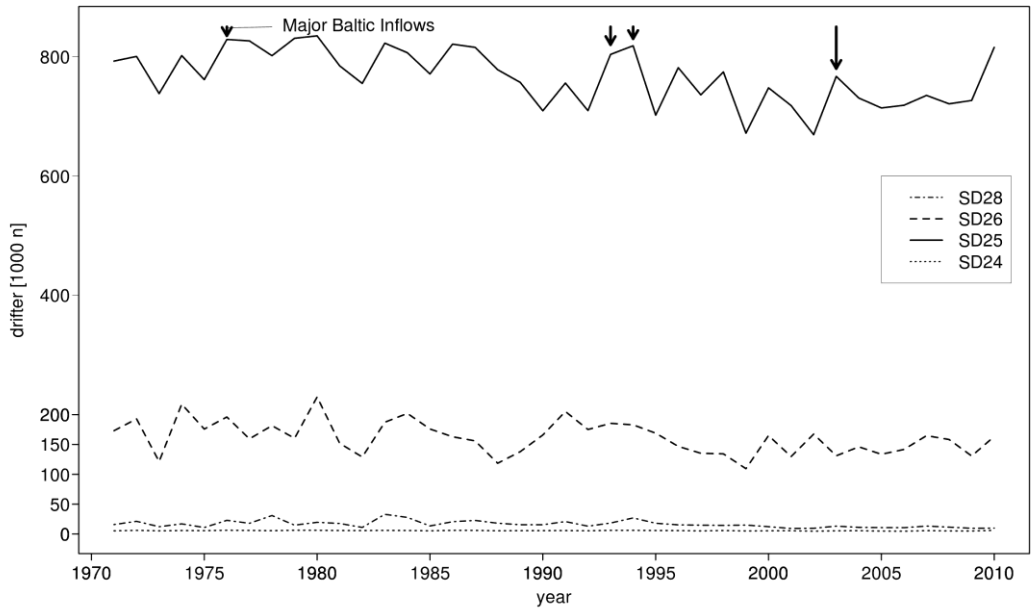

Figure 6: Annually averaged number of virtual drifters representing successfully settled Baltic cod juveniles (survivors) released in the Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28).

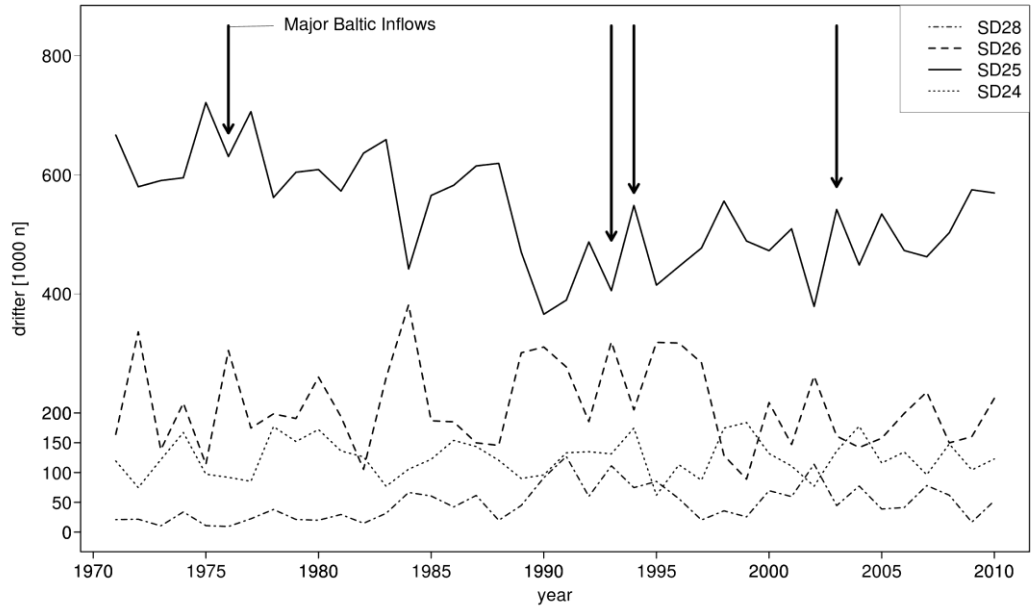

Figure 7: Annually averaged number of virtual drifters representing successfully settled Baltic cod juveniles (survivors) in the Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28).

Surviving (successfully settled) drifting particles released as first feeding larvae in the different hatching areas are shown in Fig. 6. Most settled particles have their origin in the Bornholm Basin (ICES SD 25). Compared to the Bornholm Basin, contribution of particles with origin in the Arkona Basin (ICES SD 24) and in the Gotland Basin (ICES SD 28) is only of minor importance, while a large number of particles originally released in the Gdansk Deep (ICES SD 26) successfully settled. The number of survivors (successfully settled) particles per ICES subdivisions is represented by Fig. 7. Generally, the spatial patterns showed that the number of settled particles in the Arkona Basin is relatively low.

Much higher settlement was obtained for the Bornholm Basin and for the Gdansk Deep. However, for the Bornholm Basin the model calculated higher settlement during the first half compared to the second half of the time series. Generally, low settlement was observed in the Gotland Basin, with the exception for some years in the 1990s and 2000s. The number of settled particles was found to be highly variable in all ICES subdivisions. The increase of settlement in the Arkona Basin and in the Gotland Basin was mainly due to advective larval/juvenile contribution from the adjacent hatching grounds (Bornholm Basin and Gdansk Deep).

Geographic patterns of juvenile settlement probability: For the drifting particles initially released as first feeding larvae within the different spawning grounds, the distribution of the final drifter locations revealed strong variability (Fig. 8). While for juveniles with origin in the Arkona Basin, the Bornholm Basin and the Gdansk Deep (SD 24, 25 and 26 respectively) settlement is widely dispersed, settlement of Gotland Basin (SD 28) hatched juveniles was limited to their original hatching area. Generally, only a low number of particles which hatched in the Arkona Basin and in the Gotland Basin were able to settle. Hatching in the Gotland Basin was limited to the southern part (Hinrichsen et al., 2016; their figure 9) and compared to settlement of particles released in the Bornholm Basin and in the Gdansk Deep, the number of particles which encountered optimal oxygen conditions was relatively low. Particles released in the Bornholm Basin were most widely distributed and showed the highest settlement success, while second highest settlement success and horizontal extension was obtained for particles originating in the Gdansk Deep. Generally, the highest number of particles settled in shallow waters or in the slope areas of the different ICES subdivisions. Due to frequent oxygen deficiency at the bottom of these deep basins, especially in the Gotland Basin, settlement was 1 – 2 orders of magnitude lower than in the well oxygenated shallow or slope areas.

Connectivity patterns of larval and juvenile cod: To quantify the connectivity patterns of settled particles, we calculated their retention within as well as their advective transport between ICES subdivisions (Table 2). In a long-term perspective, survival was observed to be dominated by settlement of particles in the Bornholm Basin and Gdansk Deep, i.e. the Bornholm Basin contributed on average more than 54 % and the Gdansk Deep around 11% to the overall distribution of particles. Furthermore, transport of particles with origin in the spawning ground in the Bornholm Basin contributed on average 13 and 11% to the Arkona Basin and Gdansk Deep, respectively.

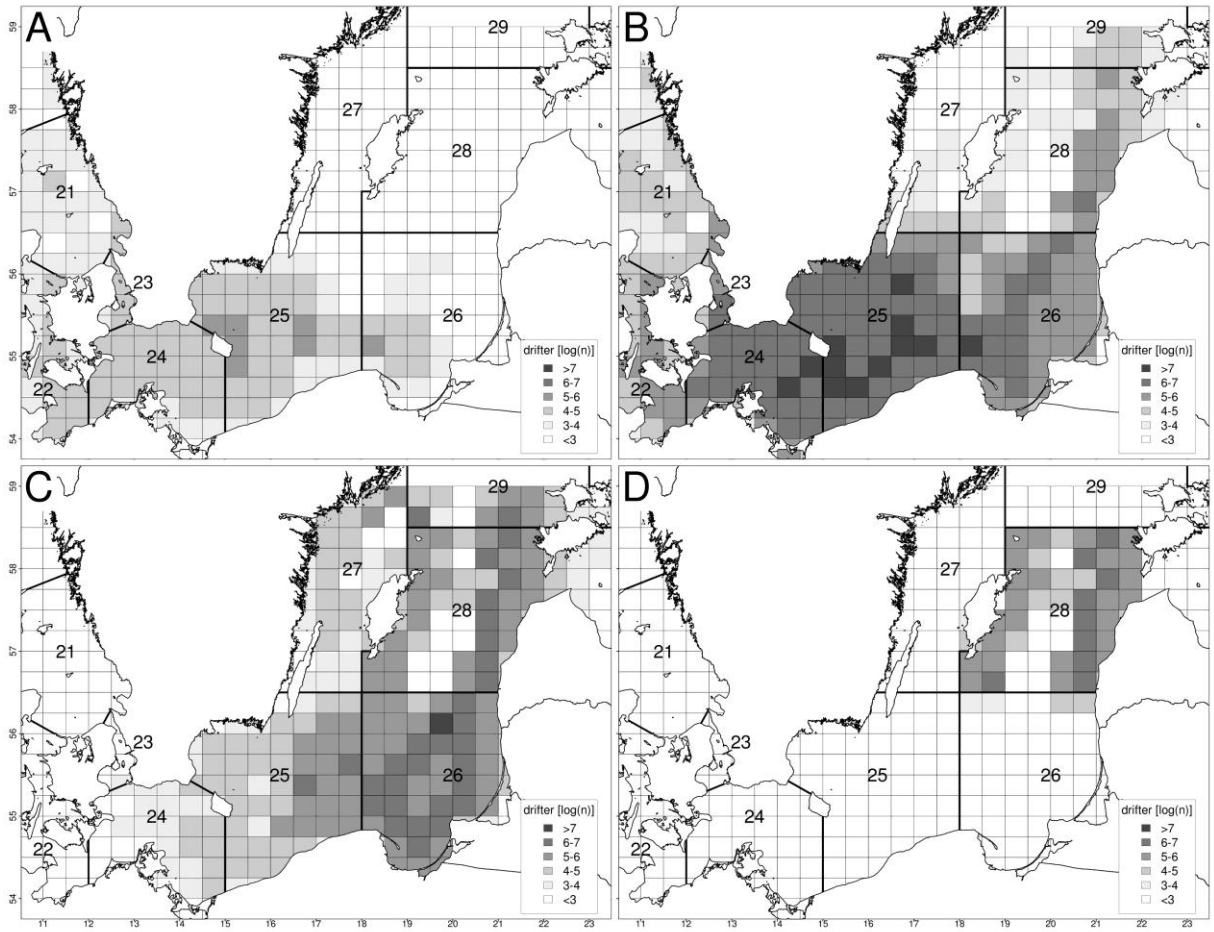

Figure 8: Horizontal distribution of virtual drifters (1971–2010) representing successfully settled Baltic cod juveniles (log10-transformed) hatched in different ICES subdivisions in the central and eastern Baltic Sea a) Arkona Basin (ICES SD 24), b) Bornholm Basin (ICES SD 25), c) in Gdansk Deep (ICES SD 26), and d) Gotland Basin (ICES SD 28).

Temporal patterns of settlement areas and observed condition of juveniles: The major part of particles in the Arkona Basin settled at depths in well oxygenated water layers above the halocline (0 - 40m; Fig. 9a). In the eastern ICES subdivisions settlement mainly took place at 40 to 70 m, i.e. the particles in the Bornholm Basin and in the Gdansk Deep predominantly settled at the edges of the basins, where the halocline hits the bottom (Fig. 9b, c; see also Fig 8b, c). Although the particles in the Gotland Basin settled in the same depth range (Fig. 9d) as in the Gdansk Deep and in the Bornholm Basin, the experienced oxygen saturation levels are totally different. In the Gotland Basin the halocline is situated deeper (80 - 110m), hence the settled particles here were exposed to less saline, but well oxygenated mixed layer water masses. Overall, the depth ranges of the drifter-derived settling points with observed occurrences of eastern Baltic cod juveniles caught during the BITS survey are similar. However, compared to the drifter-derived distribution, peak abundances of juveniles are somewhat more restricted, with lower abundances in the shallow and deepest areas (Fig. 9 a,b,c,d). Highest abundances of juvenile cod were found at depths from 35 - 50 m in all areas, which is somewhat deeper than the drifter-derived depth distribution for the Arkona Basin (Fig. 9a) and shallower for the Gdansk Deep (Fig. 9 c) and Gotland Basin (Fig. 9 d). A comparison of drifter end positions, representing potential juvenile settlement areas with the spatial distribution of catch data for juvenile

cod (age 0) from regularly conducted standard bottom trawl surveys (BITS) in the area are presented in Supplementary Material.

Table 2: Overall means and standard deviations of dispersal/retention patterns (percentages) of virtual drifters representing settled eastern Baltic juveniles. Bold numbers represent retention patterns within ICES subdivisions. West means ICES SDs further west than ICES SD 24, north means further north than SD 28.

	Drifter location at settled juvenile stage						
Spawning area	West	SD 24	SD 25	SD 26	SD 27	SD 28	North
SD 24	0.1±0.1	**0.1±0.1**	0.3±0.1	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0
SD 25	1.7±1.7	12.9±7.1	**54.6±12.1**	10.8±9.4	0.2±0.3	0.5±1.8	0.0±0.2
SD 26	0.0±0.0	0.0±0.2	1.5±2.1	**10.8±4.9**	0.1±0.5	3.8±3.7	0.8±1.6
SD 28	0.0±0.0	0.0±0.0	0.2±0.2	0.1±0.2	0.6±0.5	**0.7±0.5**	0.2±0.2

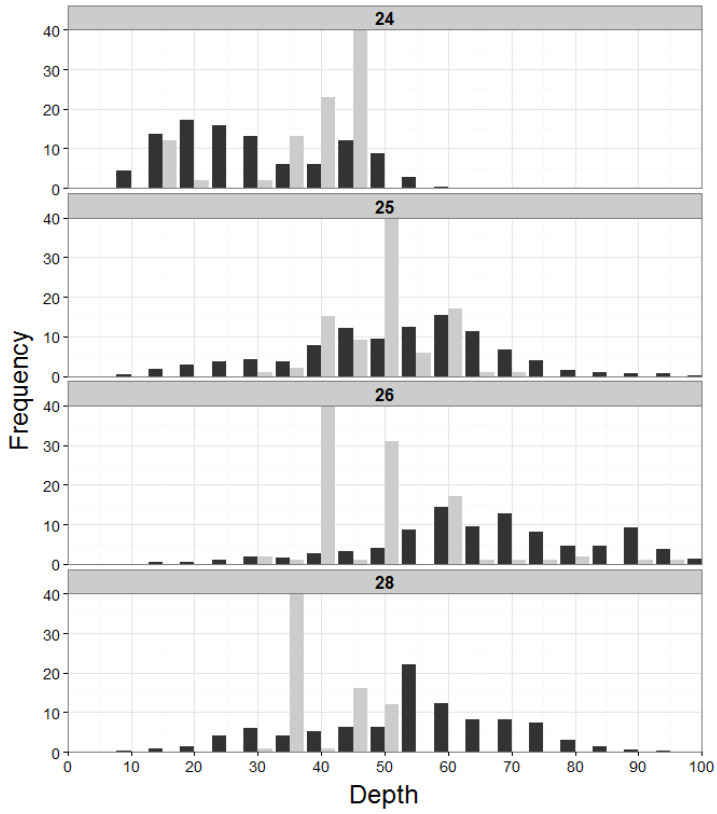

Figure 9: Observed depth distribution of settled eastern Baltic cod juveniles < 16 cm in the first quarter of the year (grey) and depth distribution of final destinations of virtual drifters representing successfully settled cod juveniles (black) in the Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), in Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28).

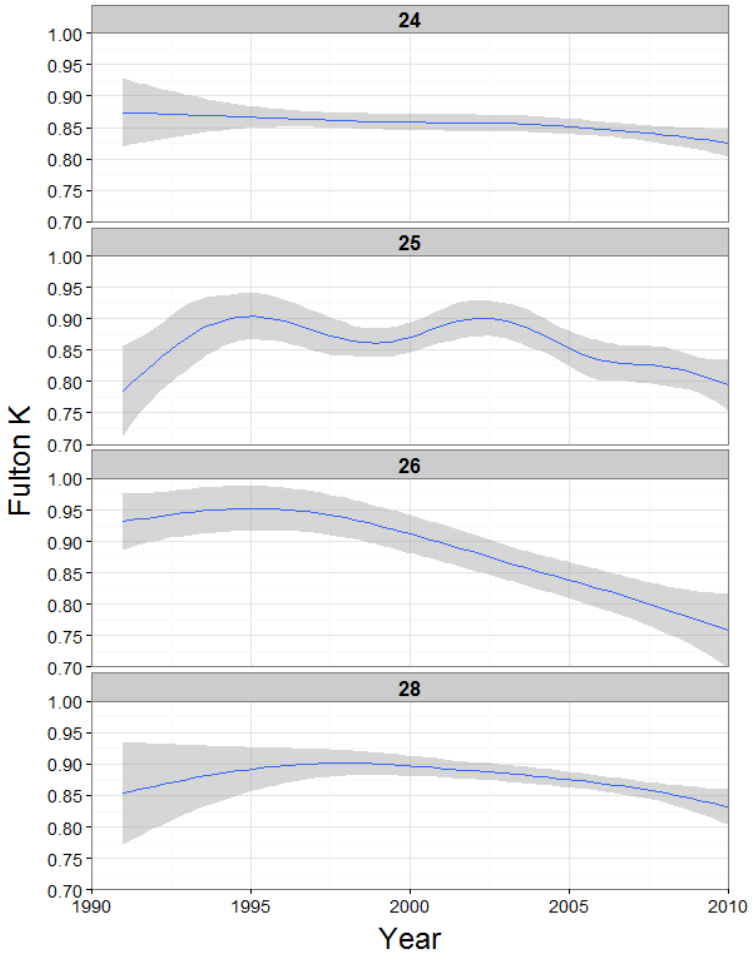

Figure 10: Fulton's K condition index of juvenile Baltic cod < 16 cm from the first quarter of the year for Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28). Plot shows mean values with 95% confidence interval band.

Somatic condition, examined as Fulton's *K* condition factor showed distinct area-specific patterns. While condition remained essentially constant over the years examined in the Arkona Basin, condition exhibited a strong negative trend in the Bornholm Basin and the Gdansk Deep, with a less pronounced negative trend in the Gotland Basin as well (Fig. 10). The time-series (1993–2010) of occupied juvenile cod habitat (Fig. 5) are strongly correlated with the Fulton's *K* condition factor (Fig. 10) for both the Bornholm Basin ($r = 0.44$, $p < 0.05$) and the Gdansk Deep ($r = 0.65$, $p < 0.05$). A similar analysis revealed that the Fulton's *K* condition factor is less correlated with the available juvenile cod habitat. Only for the Gdansk Deep a significant relationship was obtained ($r = 0.38$, $p < 0.05$).

Discussion and Conclusion

In the present study, the drift of particles representing eastern Baltic cod larvae spawned within the historically important eastern Baltic cod spawning grounds was investigated by detailed drift model simulations for the years 1971 to 2010. We have analysed where the particles changed from pelagic to demersal habitat, i.e. where the juvenile cod were able to successfully settle, thereby identifying the eastern Baltic cod nursery grounds. Furthermore, the long-term drift simulations enabled us to calculate the long-term

variability in habitat occupancy, mortalities and survival of the different eastern Baltic cod nursery grounds.

The initial distinct horizontal distribution patterns of the particles (Hinrichsen et al., 2016) as well as variations in circulation patterns facilitate mixing within different parts of the population of eastern Baltic cod (Fig. 8). Settled particles with origin in the Arkona Basin, the Bornholm Basin and the Gdansk Deep (ICES subdivisions 24, 25 and 26 respectively) are widely dispersed, especially high numbers of particles released in the Bornholm Basin were transported to nursery areas in other areas. Hüssy et al. (2016) addressed the suitability of the environmental conditions for eastern Baltic cod eggs and yolk-sac larvae in the Arkona Basin for retaining eastern Baltic cod recruits in the western Baltic Sea management unit. As cod abundance in the Arkona Basin has increased substantially since 2006, stock mixing of eastern and western Baltic has been attributed to the impact of eastern adult cod immigration (Eero et al., 2014; Hüssy et al., 2016). The present study has shown that also particles representing eastern Baltic cod juveniles settled to a relatively large extent in the western Baltic cod management area, and may significantly contribute to western Baltic cod recruitment. Thus, it is likely that not only immigration but also larval and juvenile transport could contribute to recruitment in the western Baltic Sea. It is also evident that the stock component in the Gotland Basin only to a minor degree contributed particles to nursery grounds in other areas.

Directional horizontal and vertical swimming behaviour, for example, has the potential to affect cod larval drift patterns, which could result in dispersal variability (Fiksen et al., 2007). Cod larvae and juveniles are able to actively change their vertical position in the water column which might significantly alter their drift routes, especially in wind-driven systems exhibiting a strong vertical current shear. However, as obtained from a previous study (Hinrichsen et al., 2001) and a sensitivity analysis in this study (see Supplementary Material), vertical migrations seem to have only modest effects on larval and juvenile drift patterns of Eastern Baltic cod. This is because larval cod is vertically mainly distributed in the non-directly wind-driven low ocean current velocity regime at middepth (25 to 50m), which exhibits only low differences in their end positions due to a weak vertical current velocity shear. Thus, although the drifting larvae are distributed within a wide depth range, the end positions of the particles are presumably almost independent of the initial depth at release. Observations on the vertical distribution of larval cod for most recent years, indicate that large vertical movements of larvae do not occur (Grønkjær et al., 1997). In contrast, Baltic larval sprat is directly exposed to wind-driven circulation patterns, hence their final destinations as juveniles are likely more affected by vertical migration (Hinrichsen et al., 2005).

Also horizontal swimming behaviour has the potential to affect the final distribution of cod larvae (Werner et al. 1993, Fiksen et al. 2007). In practice though, the potential for this kind of behaviour to change the spatial patterns observed at the scale of observation of our study is probably low. Sustained net displacements of cod larvae have been estimated to be around 0.6-1.2 cm s^{-1} (Lough and Bolz 1989, Stanley et al. 2012), corresponding to 500-1000 m day^{-1} and 30-60 km during the course of the modelled larval phase. This would not

affect the observed larger-scale patterns found of this study. Horizontal swimming has therefore been assumed to be of less importance compared to the horizontal flow.

Suitable habitat for juvenile cod settlement can be found in both shallower waters as well as in the deeper part of the central Baltic Sea. While high frequencies of hypoxia were found in the deep basin areas of the Bornholm Basin for the time period 1971-2010, the Gdansk Deep and the Gotland Basin, anoxia was mainly limited to the eastern and western Gotland Basin (Lehmann et al., 2014; Hinrichsen et al., 2016). However, the areas of available and occupied habitat increased significantly only in the deeper central part of the Bornholm Basin during inflow and post-inflow situations (1976, 1993, 1994, 2003), when high-saline and well-oxygenated water masses from the North Sea and western Baltic enlarged the habitats. The area providing favorable settling conditions for juvenile cod, determined as size of the area with bottom oxygen saturation > 60% as well as the area where juveniles successfully settled, declined significantly over the last 40 years in the major nursery grounds (Bornholm Basin and Gdansk Deep) from 1970 to 2010. Transport to these suitable nursery areas and away from areas with high adult cod abundance may be an important process governing juvenile growth and survival (Köster et al., 2016). Density-dependent processes operating after the onset of juvenile settlement may be of substantially greater importance if the spatial extent of the habitat for Baltic cod juveniles decreases as a result of deteriorating oxygen concentrations (Hinrichsen et al., 2011). Such trends will probably continue, because general improvements in the environmental conditions necessary for successful cod spawning and a growing juvenile habitat area is not to be expected in the 21st century (BACC Author Team, 2006).

A comparison of particle settlement depths with observed depth distribution of juvenile cod caught during the BITS surveys in the first quarter of the year generally confirms the accuracy of the model's predictions. Generally, a direct comparison of spatially resolved field caught juvenile distributions and the output of drift model simulations might be difficult. A comparison of juvenile drifter end positions with catch data showed a high degree of concurrence. However, in the shallow coastal areas of the Bornholm Basin large fractions of simulated particles were found, but without corresponding juvenile occurrence. One reason is that simulated particle end positions represent a relative, general pattern of particles released in the spawning areas of the eastern Baltic cod compared to juvenile catches. The latter are based on actual abundance data and thus indirectly on stock structure (e.g. spawning stock biomass, timing of spawning, fecundity, larval mortality). Secondly, juvenile catches in the ICES subdivisions 24 to 28 might also include advective mixing of juveniles originating from different Baltic cod stocks. E.g. high larval and juveniles transport of western Baltic cod into the Arkona and Bornholm Basin (~10%) is described in Huwer et al, (2016), which might affect the total juvenile population in these areas. Additionally, habitat choice and habitat-specific mortality rates may have affected the spatial distribution of the juveniles (up to 16 cm length) caught in the BITS survey compared to the settlement estimates from our simulations. For example, differences in mortality rates due to cannibalism from larger cod (Uzars and Plikshs, 2000, Köster et al., 2016), and active habitat choice to either avoid predators or to find optimal foraging conditions may have significant effects on the distribution of the juveniles after settlement (Nielsen et al. 2013, Casini et al. 2016). For example, the sampling methodology for

juvenile cod is not free of other sources of uncertainty. For example, the sampled fish data may be biased due to a size-selectivity of the sampling gear, or that avoidance is a function of size and condition. Furthermore, true zero-catches of juveniles close to land (see Fig. SM2) could be an indication of a directional migration towards deeper areas for larvae settled in coastal areas.

From sensitivity analysis it also became evident that the mean horizontal distribution of field caught juveniles fits relatively well to the model output when initial release fields based on egg and yolk-sac larval mortality were used to run the drift model. In contrast, if homogenously distributed release fields like in a previous study (Hinrichsen et al., 2009) were used, a missing mortality acting during the egg and yolk-sac larval phase results in an overestimation of the simulated mean particle distribution in the Gdansk Deep and the Gotland Basin.

Besides the refinement of the horizontal resolution of the hydrodynamic model (~2.5 km), similar to the study performed by Hinrichsen et al. (2009), the modelling exercise utilized the same extension of spawning areas and initial vertical distribution of larvae. Furthermore, the drift model was run for almost the same release events, but for a more extended time period (1971-2010). In contrast to the previous study the larvae were not seeded homogeneously on regular grids, instead spatial variability in egg and yolk-sac larval survival was taken into account, i.e. differences in seeding densities within and between areas (Hinrichsen et al., 2016). The motivation to change to these egg and yolk-sac larval mortality dependent initial release fields is based on the agreement between the mean spatial distribution of yolk-sac larval survivors back-tracked to their spawning locations (Hinrichsen et al., 2016; their Fig. 8) and an observed mean cod egg stage Ia distribution in the Bornholm Basin (Hinrichsen et al,, 2007).

To obtain a proxy for the settlement habitat quality related to oxygen conditions for eastern Baltic juvenile cod, Hinrichsen et al. (2009) used monthly mean oxygen profiles for ICES subdivisions provided by the ICES oceanographic data base. In contrast, for this study, spatially and temporally highly-resolved hydrodynamic model-based oxygen distributions (Lehmann et al., 2014) were available, providing much more precise estimates of oxygen-related mortality. In the current exercise also some minor changes to the previous study regarding settlement rules have been included. Knowledge on the minimum oxygen saturation levels required by cod juveniles for settlement is however less certain (e.g. Chabot and Dutil, 1999; Neuenfeldt, pers. communication). Any uncertainty of the oxygen-saturation requirement for settlement could also have an impact on the drift patterns and hence on the end positions of particles. However, the results of a sensitivity analysis on this topic revealed only slightly different settlement patterns, when the model parameter value (minimum required oxygen saturation for settlement) were modified. Similar to Hinrichsen et al. (2009), it remains unclear how pelagic juveniles will behave when encountering low oxygen at the bottom while intending to settle. Will the juveniles simply continue to stay pelagic or will they move upslope to find more favourable environmental conditions in terms of sufficient oxygen saturation?

Evidence exists that growth of settled juvenile Baltic cod may be affected by density-dependent processes such as competition for food (Hüssy et al., 2003) and cannibalism

(Uzars and Plikshs, 2000). Field data on Fulton's *K* condition factor of juvenile cod (Fig. 10) showed similar declining trends over the past 18 years in the eastern part of the Baltic Sea as for habitat occupancy (Fig. 5). Correlations between these time series revealed a strong relationship both in the Bornholm Basin and in the Gdansk Deep. This indicates that the decrease in juvenile cod condition might be the result of the observed habitat reduction due to deteriorating oxygen conditions, and may confirm the importance of density dependence as a recruitment-related process. A decrease in habitat availability would compress juveniles into smaller nursery areas, since the abundance of juveniles has increased slightly during the same time (ICES, 2016). Both, the general weak correlation of available habitat as well as the relatively high correlation of occupied habitat of juvenile drifter with the Fulton's *K* condition factor indicates that settlement success might not be irrespective of ocean circulation. Hence, juvenile fish habitat information could provide independent insight into the variability of early-life stage dynamics and potential recruitment success and could also support the utility of hydrodynamic models for fishery management (Hinrichsen et al., 2011). A recent study of spatio-temporal dynamics of condition in eastern Baltic cod found similar patterns as those presented in the present study not only for juveniles, but for all length classes of eastern Baltic cod (Casini et al., 2016). These changes were attributed to density-dependent food limitation as a result of hypoxia-related decrease in suitable habitat, thereby supporting our hypothesis of a causal link between available habitat and condition. An increase in juvenile Baltic cod settlement probability as well as an increase of the Fulton´s *K* condition factor could be expected only after an improvement in habitat suitability based on oxygen concentration, such as after the major Baltic inflows in 1993 and 2003. Such patterns were indeed observed in the Bornholm Basin, but not in the other nursery areas.

Studies from the 1990s and 2000s identified the key controlling factors for eastern Baltic cod recruitment to be major Baltic inflows of saline oxygen-rich water from the North Sea in combination with oxygen consumption (MacKenzie et al., 1996; Köster et al., 2005), as well as prey availability for first feeding larvae (Hinrichsen et al., 2002; Möllmann et al., 2005). Habitat availability for successful juvenile settlement as obtained from this study could be included in statistical analyses to i) identify their importance compared to other potential larval mortalities (e.g. food availability, predation) or ii) as it has been suggested as a potential second order regulating factor for recruitment (Köster et al. 2016). Hence, spatially and temporally resolved information on settlement area size as obtained from the present study could be a good candidate to be involved in future recruitment studies for an improved understanding of regulating processes.

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Supplementary Material

Comparison between in situ oxygen measurements and BSIOM model oxygen fields. In situ oxygen measurements for the Bornholm Basin area were downloaded from the ICES Oceanographic data base (available at http://ocean.ices.dk/HydChem, ICES, 2009). All data for the modelled period between 1971 and 2010 were compiled and aggregated with measurements treated as outliers when outside of 3 time mean error distance. Aggregation was performed into monthly mean 1m resolved profiles of the entire Bornholm Basin. These profiles were further aggregated into 3 vertical depth layers of 0-41, 41-77 and 77-110m, respectively, resulting into 3 monthly time series of oceanographic distinct layers. They can be understood as the upper mixed layer of low salinity, the deep basin layer that is cut off from direct influences of the atmosphere and the highly variable layer in the middle containing the permanent halocline. Oxygen data from the BSIOM model data used in the present study was aggregated in the same way and correlated with the direct oxygen measurements from the ICES collective data base (see Table SM1 and Figure SM1). Within the relevant depth layers for this study above 77m where the larval drift was modelled, high positive correlations were obtained. The model seams to almost perfectly mimic the atmosphere mixed layer dynamics (adj $R^2 = 0.829$). Here mainly the temperature changes alter the oxygen solubility in the Baltic Sea water and wind driven mixing effects make the upper 40m quite homogenous. Within the depth layer containing the permanent halocline characteristics from bottom waters, with hypoxic and from the top layer with fully oxygenated conditions, become mixed. Here small changes in hydrographic conditions translate into possibly significant changes of the oxygen conditions. Due to the not ideal horizontal coverage of the in-situ measurements, their various error sources and additionally the smoothing nature of the oceanographic model, the obtained fit of two oxygen time series of adj. $R^2 = 0.523$ has to be considered as reasonable statistical approach. In conclusion are the modelled fields of oxygen conditions in this study a confident approximation of actual conditions.

Table SM1: Coefficients and parameters of correlations between in situ oxygen measurements taken from the ICES Oceanographic data base and simulated oxygen data from the oceanographic model (BSIOM) used in the present study. Correlations were performed within 3 different vertical depth layers in the Bornholm Basin area of 0-41, 41-77 and 77-110m, respectively.

layer	intercept	slope	adj. R^2	df	p
0 – 41	-0.235	1.032	0.829	486	<.001
41 – 77	-2.598	1.218	0.523	483	<.001
77 – 110	0.24	0.408	0.324	458	<.001

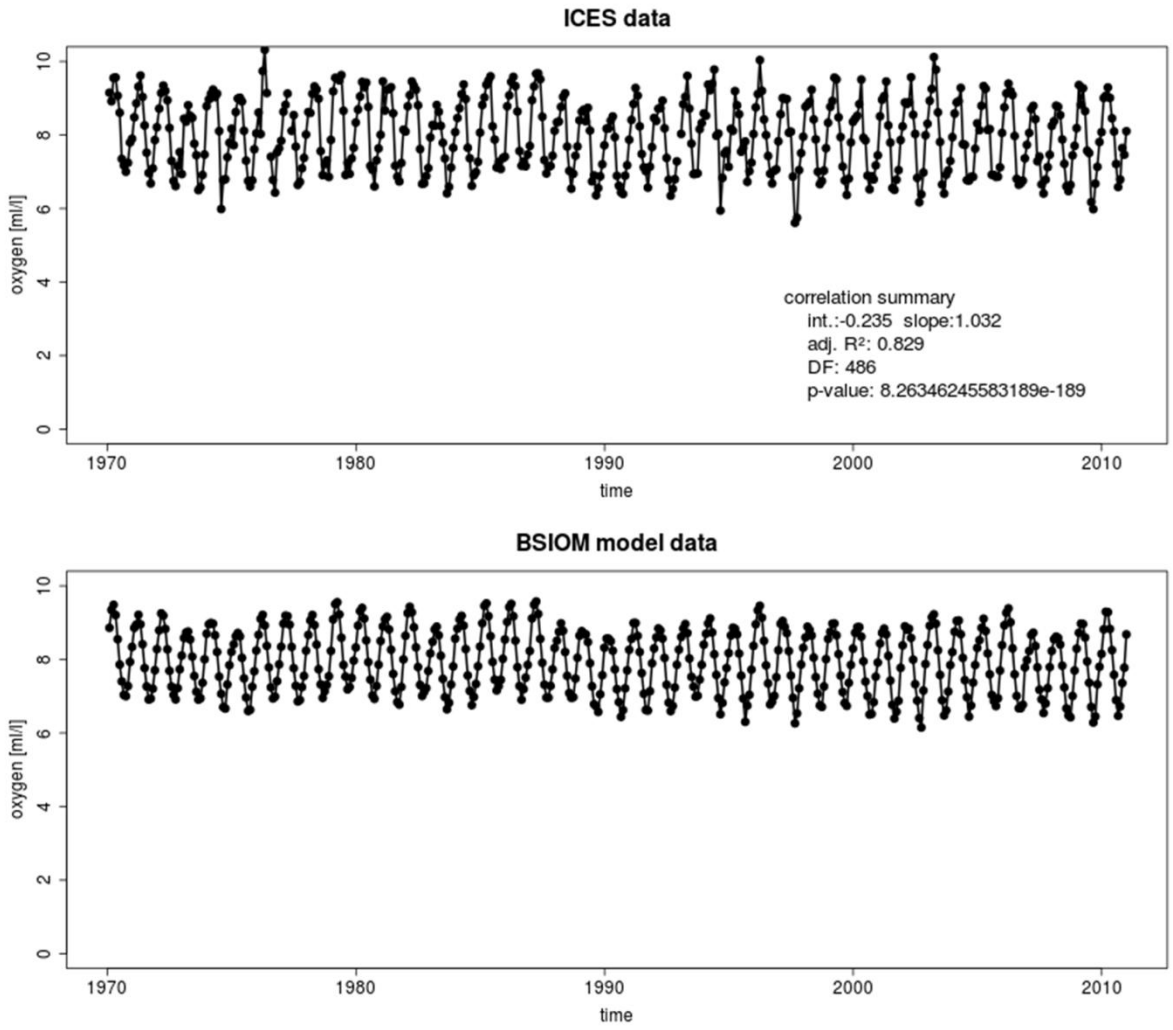


Figure SM1: Monthly time series of oxygen content in the depth layer between 0 and 41m in the Bornholm Basin. Top panel shows time series derived from in situ oxygen measurements taken from the ICES Oceanographic data base and bottom panel shows equal aggregation of oxygen fields produced by the BSIOM oceanographic model.

Comparison of drifter end positions with spatial distribution of juvenile cod: In order to validate the results from the drift modeling exercise, we produced maps of drifter end positions, representing a long-term mean data set of potential juvenile settlement areas (Fig. SM2). We compared them with the spatial distribution of catch data for juvenile cod (Fig. SM3) obtained from regularly conducted standard bottom trawl surveys in the area (see main document). The catch data are the same as used for the calculation of the Fulton's *K* condition factor. The horizontal maps were constructed by simply counting the number of field caught juveniles and particle drift endpoints obtained from hydrodynamic model simulations in rectangles of approximately 50 x 50 km size for the time period from 1991-2010. To allow direct comparisons, the numbers found in the rectangles were normalized by dividing them with respect to the maximum number of field caught juveniles or juvenile drift endpoints found in the whole area (ICES subdivisions 24 to 28).

The comparison of drifter end positions with catch data showed a high degree of concurrence. In the Gdansk Deep and in the Gotland Basin the simulated particles as well as field caught juveniles were mainly found at the shallower edges of the basins and never

in the generally anoxic or hypoxic deep water areas. In the shallow coastal areas of the Bornholm Basin large fractions of simulated particles were found, but no corresponding juvenile occurrence. Additionally, similar to a previous study performed by Hinrichsen et al. (2009) we produced a map of drifter end positions, representing potential juvenile settlement areas based on feeding larvae release fields without utilization of mortality during the egg and yolk-sac larval stage (Fig. SM4). It is remarkable that the mean horizontal distribution of field caught juveniles fits relatively well to the model output when in the initial release fields egg and yolk-sac larval mortality was included in the drift model runs (Fig. SM4). In contrast, if homogenously distributed release fields like in a previous study (Hinrichsen et al., 2009) without utilization of egg and yolk-sac larval mortality were used (Fig. SM2), higher normalized abundances of the simulated mean particle distribution in the Gdansk Deep and the Gotland Basin were obtained. A spatial overlap coefficient as developed by Horn (1966) revealed high agreement between observations and simulations (0.78), if only the number of grid boxes was taken into account, where juveniles were caught and simulated particles settled. Despite of inclusion of spatially resolved abundance data of juvenile cod and only homogenously distributed initial release fields of simulated first feeding larvae, the spatial overlap coefficient resulted in an unexpected high value (0.39). However, inclusion of abiotic mortality processes (Hinrichsen et al., 2016) improved the spatial overlap coefficient by 10% and could be seen as an improvement compared to the results obtained from the modelling approach performed by Hinrichsen et al. (2009).

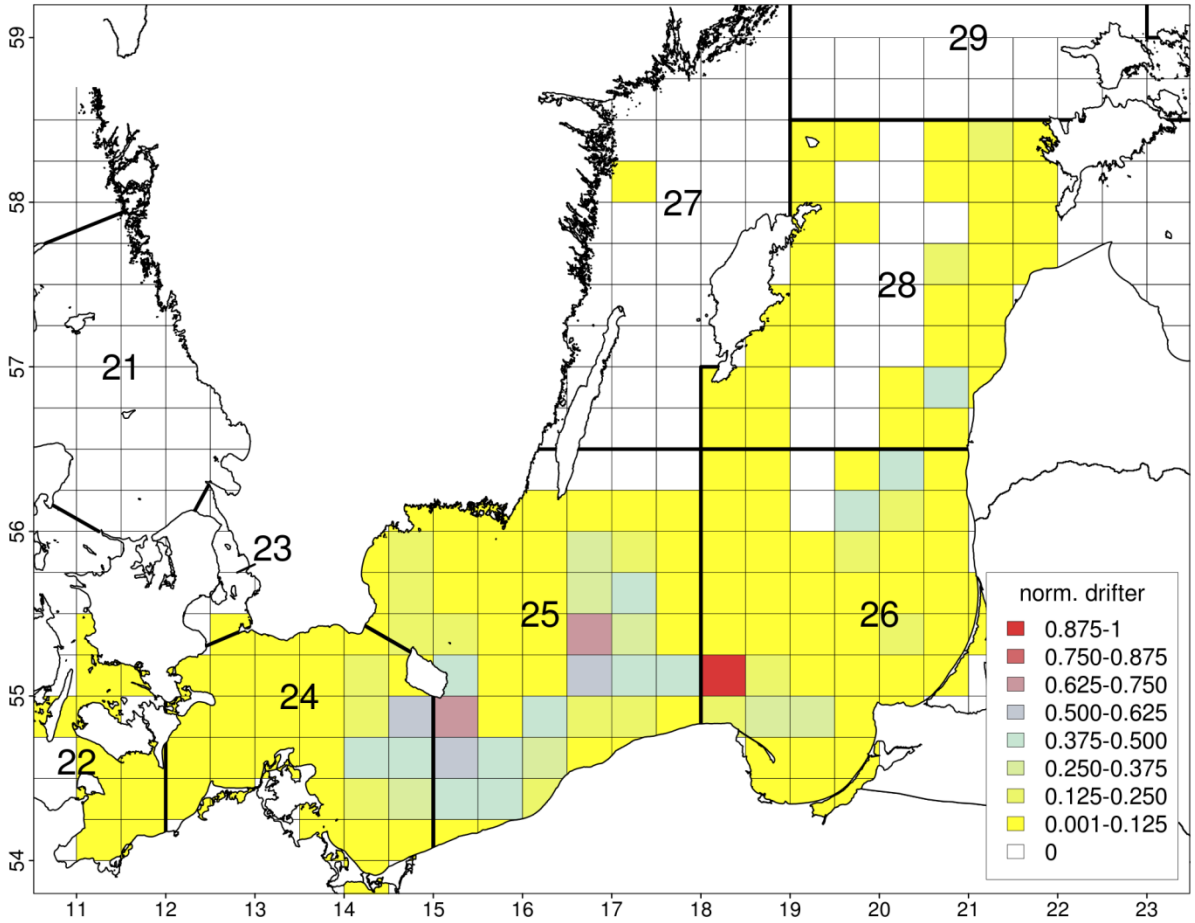


Figure SM2: Horizontal distribution of virtual drifters (1991-2010) representing successfully settled Baltic cod juveniles hatched in different ICES subdivisions in the central and eastern Baltic Sea: Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28). The initial release distribution pattern is based on differences in environmental-related mortality sources, thus giving rise to an unequal amount of drifters per hatching area (Hinrichsen et al., 2016). White boxes represent true zeros and not a lack of data.

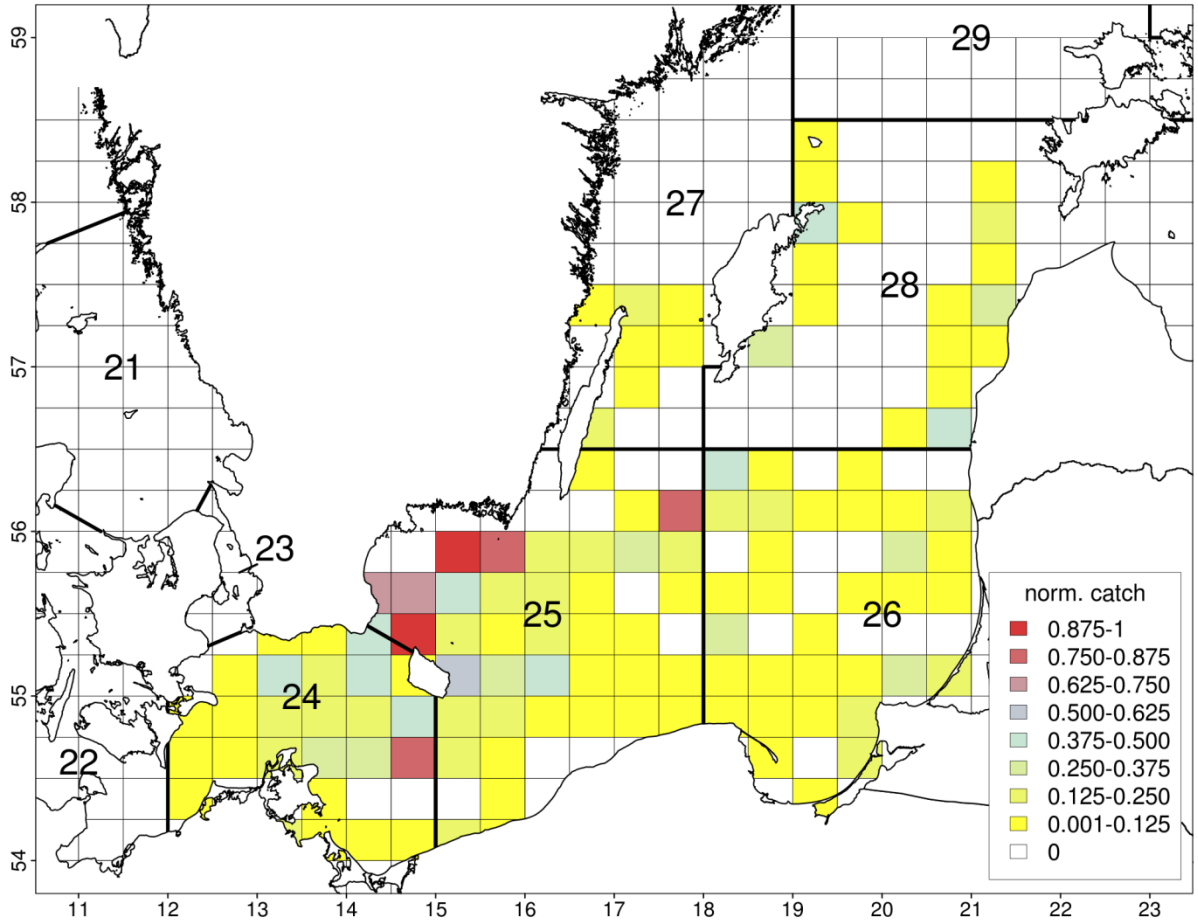


Figure SM3: Horizontal distribution of Baltic cod juveniles (1991-2010) caught in different ICES subdivisions in the central and eastern Baltic Sea: Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28). White boxes represent true zeros and not a lack of data.

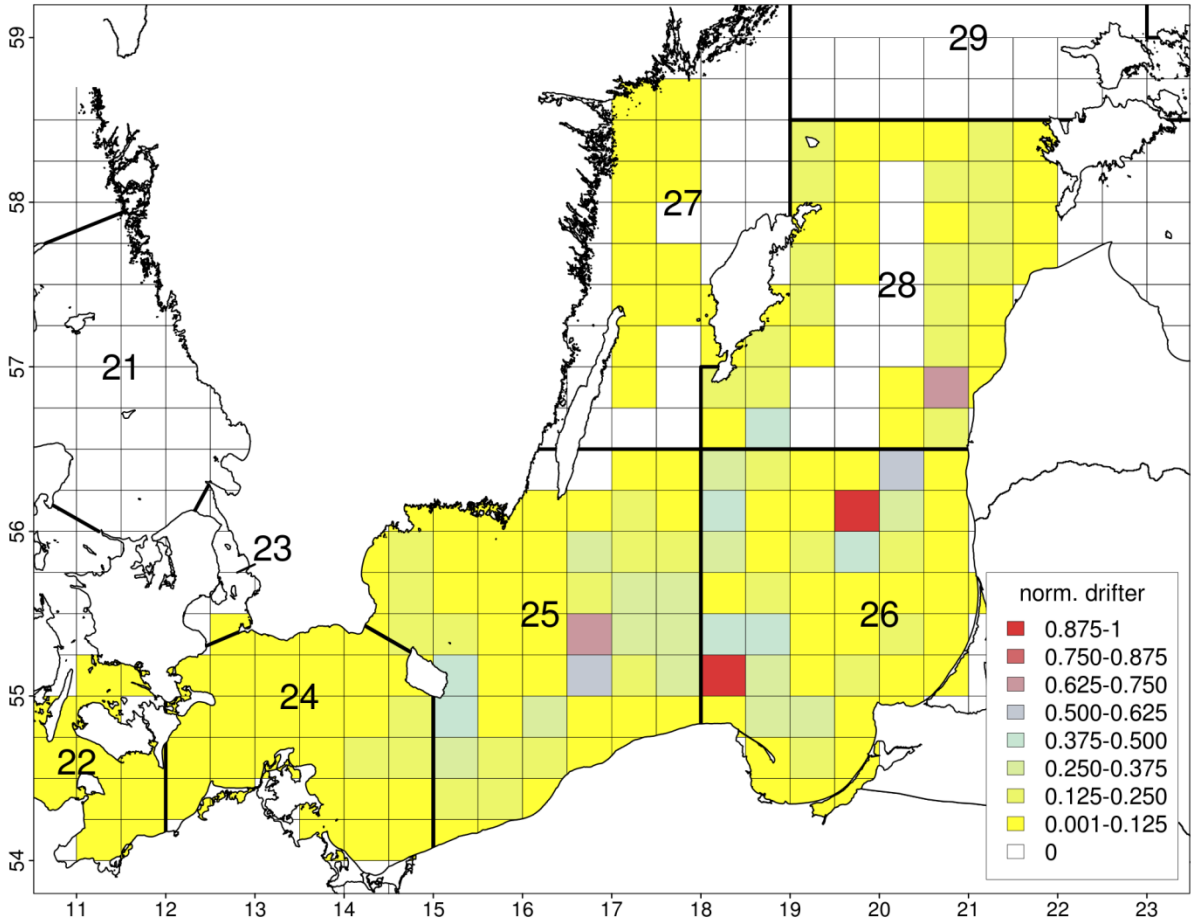


Figure SM4: Horizontal distribution of virtual drifters (1991-2010) representing successfully settled Baltic cod juveniles hatched in different ICES subdivisions in the central and eastern Baltic Sea: Arkona Basin (ICES SD 24), Bornholm Basin (ICES SD 25), Gdansk Deep (ICES SD 26), and Gotland Basin (ICES SD 28). The initial release distribution pattern is based on an equal amount of drifters per hatching area. White boxes represent true zeros and not a lack of data.

Sensitivity analyses on the biophysical model: A measure for the quality of our model results is to examine how the uncertainty in the description of parameter fields translates into deviations of juvenile settlement probability compared with reference values obtained by our standard model runs. For this purpose, we have analyzed how the vertical larval distribution pattern and modifications of the required oxygen saturation levels for successful settlement could potentially alter their final destinations and transport to suitable habitat.

Impact of the vertical distribution patterns on travelled distances of successfully settled juveniles: One example of the potential impact of vertical larval migration schemes of eastern Baltic cod on the spatial distribution of their end positions after a certain time of drift is published in Hinrichsen et al. (2001). Besides this previous study we also analyzed the variability of the end positions if the feeding larvae were initially released at different depths. For this purpose we have only calculated the mean distances between the end positions of successfully settled juveniles released as feeding larvae drifters at the same geographical positions but different depths (26.25-48.75m). The distances between the different end positions were calculated relative to the end positions of those drifters

initially released at the uppermost release depth level (26.25m). As obtained from Fig. SM5 the distances between these juvenile end positions are on average relatively low, hence the impact of the vertical distribution and hence also any vertical migration of larvae on their transport could be expected low.

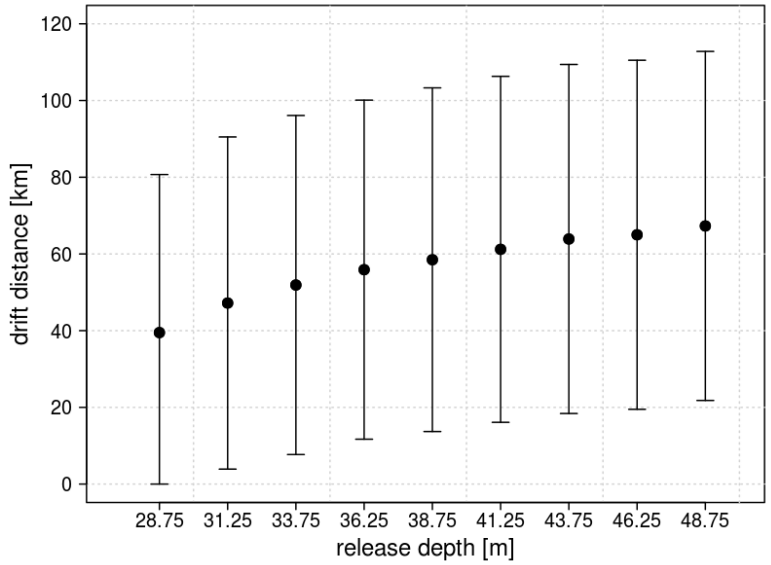


Figure SM5: Mean distances of Baltic cod juvenile settlement locations (initially released at the same positions but different release depth) relative to initial release depth (26.25m).

Impact of oxygen saturation levels on Baltic cod juvenile settlement: Specific information about oxygen preference or tolerance of eastern Baltic cod juveniles at the stage of settlement is not available. In this study, the environmental threshold level for juvenile settlement was based on recent, preliminary investigations (minimum of 60% oxygen saturation required at settlement; Neuenfeldt, pers. comm.). In order to examine the implication of the uncertainty of oxygen saturation levels on settlement probability, the parameter value was altered by $\pm$10% (Fig. SM6). As expected these changes in oxygen saturation are related negatively to the number of successfully settled juvenile drifters: a 10% decrease leads on average to an increase of 3.6% and a 10% increase on average to a decrease of 7.7% of settled juvenile drifters.

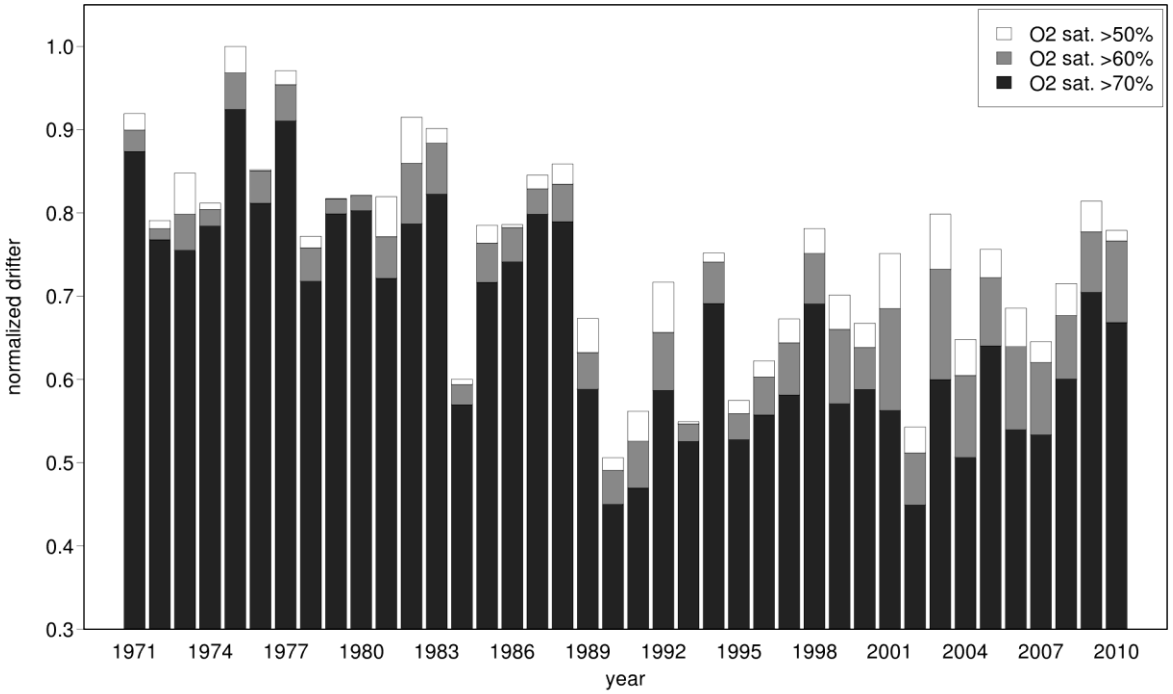


Figure SM6: Normalized annually averaged virtual drifters representing successfully settled Baltic cod juveniles in the Bornholm Basin (ICES SD 25) for different required oxygen saturation levels (50, 60, 70%).

References (Supplementary Material)

Hinrichsen, H-H., St John, M.A., Aro, E., Grønkjær, P., Voss, R., 2001. Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. ICES Journal of Marine Science 58, 973–984.

Hinrichsen, H-H., Kraus, G., Böttcher, U., Köster, F., 2009. Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: knowledge for the design of Marine Protected Areas. ICES Journal of Marine Science 66, 101–108.

Hinrichsen, H.-H., Lehmann, A., Petereit, C., Nissling, A., Ustups, D., Bergström, U., Hüssy, K., 2016. Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. Progress in Oceanography, 143, 13-25

Horn, H.S., 1966. Measurements of 'overlap' in comparative ecological studies. Am. Nat. 100, 419-424.

ICES, 2009. ICES Dataset on Ocean Hydrography. The International Council for the Exploration of the Sea, Copenhagen 2009

References (Chapter 2)

Bagge, O., Thurow, F., Steffensen, E., Bay, J., 1994. The Baltic cod. Dana 10, 1–28.

Bleil, M., Oeberst, R., Urrutia, P., 2009. Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. Journal of Applied Ichthyology, 25, 10–17.

Bumke, K., Karger, U., Hasse, L. Niekamp, K., 1998. Evaporation over the Baltic Sea as an example of a semi-enclosed sea. Contr. Atmos. Phys., 71(2), 249-261.

Casini, M., Cardinale, M., Hjelm, J., 2006. Inter-annual variation in herring, Clupea harengus, and sprat, Sprattus sprattus, condition in the central Baltic Sea: what gives the tune? Oikos 112, 638–650.

Casini, C., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., Lundström, K., Neuenfeldt, S., Gårdmark, A., Hjelm, J., 2016.Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. Royal Society Open Science. 3:160416.

Chabot, D., Dutil, J.-D., 1999. Reduced growth of Atlantic cod in non-lethal hypoxic conditions Journal of Fish Biology, 55(3), 472-491.

Eero, M., Hemmer-Hansen, J., Hüssy, K., 2014. Implications of stock recovery for a neighbouring management unit: experience from the Baltic cod, 58, 1356-1370. ICES Journal of Marine Science, 71: 1458–1466

Eero, M., Hjelm, J., Behrens, J., Buchmann, K., Cardinale, M., Casini, M., Gasyukov, P. et al. 2015. Eastern Baltic cod in distress: biological changes and challenges for stock assessment. ICES Journal of Marine Science, 72: 2180–2186.

Fiksen, Ø., Jørgensen, C. Kristiansen, T., Vikebø, F., Huse, G., 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Marine Ecoloy Progress Series, 347: 195-205.

Gallego, A., North, E.W., Pettigas, P., 2007. Introduction: status and future of modelling physical-biological interactions during the early life of fishes. Marine Ecology Progress Series 347, 121–126.

Grønkjær, P., Clemmesen, C., St. John, M., 1997. Nutritional condition and vertical distribution of Baltic cod larvae. Journal of Fish Biology, 51A, 352-369.

Hay, D.E., McCarter, P.B., DDaniel, K.S., 2001. Tagging of Pacific herring Clupea pallasi from 1936-1992: a review with comments on homing, geographic fidelity, and starying. Canadian Journal of Fisheries and Aquatic Science

Heath, M.R., Gallego, A., 1998. Bio-physical modelling of the early life stages of haddock, Melanogrammus aeglefinus, in the North Sea. Fisheries Oceanography, 7(4), 110 – 125.

Hinrichsen, H.-H., Lehmann, A., St.John, M.S., Brügge, B., 1997. Modeling the cod larvae drift in the Bornholm Basin in summer 1994. Cont. Shelf Res. 17, 1765–1784.

Hinrichsen, H-H., St John, M.A., Aro, E., Grønkjær, P., Voss, R., 2001. Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation. ICES Journal of Marine Science 58, 973–984.

Hinrichsen, H-H., Möllmann, C., Köster, F.W., Kornilovs, G., 2002. Biophysical modelling of larval Baltic cod (Gadus morhua) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 59, 1858–1873.

Hinrichsen, H-H., Böttcher, U., Köster, F.W., Lehmann, A., St. John, M.A., 2003. Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. Journal of Sea Research 49, 187–201.

Hinrichsen, H.-H., Kraus, G., Voss, R., Stepputtis, D., Baumann, H., 2005. The general distribution pattern and mixing probability of Baltic sprat juvenile populations. Journal of Marine Systems 58(1-2), 52–66.

Hinrichsen, H.-H., Voss, R., Wieland, K., Köster, F., Andersen, K.H., Margonski, P., 2007. Spatial and temporal heterogeneity of the cod spawning environment in the Bornholm Basin, Baltic Sea. Marine Ecology Progress Series, 345: 245-254.

Hinrichsen, H-H., Kraus, G., Böttcher, U., Köster, F., 2009. Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: knowledge for the design of Marine Protected Areas. ICES Journal of Marine Science 66, 101–108.

Hinrichsen, H-H., Dickey-Collas, M., Huret, M., Peck, M.A., Vikebo, F.B., 2011. Evaluating the suitability of coupled biophysical models for fishery management. ICES Journal of Marine Science 68, 1478–1487.

Hinrichsen, H.-H., Huwer, B., Makarchouk, A., Petereit, C., Schaber, M., Voss, R. 2011 Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (Gadus morhua). ICES Journal of Marine Science 68(10), 2019 – 2028.

Hinrichsen, H-H., Hüssy, K., Huwer, B., 2012. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics ICES Journal of Marine Science 69, 1744-1752.

Hinrichsen, H.-H., Lehmann, A., Petereit, C., Nissling, A., Ustups, D., Bergström, U., and Hüssy, K., 2016. Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. Progress in Oceanography, 143, 13-25

Hüssy, K., St.John, M., Boettcher, U. 1997 Food resource utilization by juvenile baltic cod gadus morhua: A mechanism potentially influencing recruitment success at the demersal juvenile stage? Marine Ecology Progress Series 155, 199-208.

Hüssy, K., Hinrichsen, H-H., Huwer, B., 2012. Hydrographic influence on the spawning habitat suitability of western Baltic cod (Gadus morhua) ICES Journal of Marine Science 69, 1736-1743.

Hüssy, K., Hinrichsen, H.-H., Mosegard, H., Eero, M., Hemmer Hansen, J., Lehmann, A., Scherffenberg Lundgaard, L., 2016. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment. ICES Journal of Marine Science, 73(2), 293-303.

Huwer, B., Hinrichsen, H.-H., Hüssy, K., Eero, M., 2016. Connectivity of larval cod in the transition area between North Sea and Baltic Sea and potential implications for fisheries management. ICES Journal of Marine Science 73, 1815-1824.

ICES 2016. Report oft the Baltic Fisheries Assessment Working Group (WGBFAS)

Köster, F. W., Möllmann, C., Hinrichsen, H-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., 2005. Baltic cod recruitment - the impact of climate variability on key processes. ICES Journal of Marine Science 62, 1408–1425.

Köster, F.W., Huwer, B., Hinrichsen, H.-H., Neumann, V., Makarchouk, Eero, M., von Dewitz, B., Hüssy, K., Plikshs, M., 2016. Eastern Baltic cod recruitment revisited—dynamics and impacting factors. ICES Journal of Marine Science, DOI: 10.1093/icesjms/fsw172

Kronsell, J., Andersson, P., 2012. Total regional runoff to the Baltic Sea. HELCOM Indicator Fact Sheets 2011. Online. (http://www.helcom.fi/environment2/ifs).

Lehmann, A., Hinrichsen, H.-H., 2000. On the thermohaline variability of the Baltic Sea. Journal of Marine Systems 25, 333–357.

Lehmann, A., Krauß, W., Hinrichsen, H-H., 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus 54A, 299–316.

Lehmann, A., Hinrichsen, H.-H., Getzlaff, K., Myrberg, K., 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. Journal of Marine Systems, 134:20-28.

Lough, R. G., Bolz, G. R., 1989. The movement of cod and haddock larvae onto the shoals of Georges Bank. Journal of Fish Biology, 35(sA), 71-79.

MacKenzie, B.R., St. John, M.A., Wieland, K., 1996. Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. Marine Ecology Progress Series 134, 265–281.

Maczassek, K., 2006. Feeding ecology of the cod (Gadus morhua L.) in the central Baltic Sea. Dipl. Thesis (in german), Department of Fishery Biology, GEOMAR, Kiel; Germany

Miller, T., 2007. Contribution of individual-based coupled physical-biological models to understand recruitment in marine fish populations. Marine Ecology Progress Series 347, 121–126.

Nielsen, J. R., Lundgren, B., Kristensen, K., and Bastardie, F. (2013). Localisation of nursery areas based on comparative analyses of the horizontal and vertical distribution patterns of juvenile Baltic Cod (Gadus morhua). PloS one, 8(8), e70668.

Nissling, A., Westin, L., 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. Marine Ecology Progress Series 152, 261–271.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W., 2005. Climate, zooplankton and pelagic fish growth in the central Baltic Sea. ICES Journal of Marine Science, 62, 1270-1280.

Novotny, K., Liebsch, G., Lehmann, A., Dietrich, R., 2006. Variability of sea surface heights in the Baltic Sea: An intercomparison of observations and model simulations, Marine Geodesy, 29, 113-134.

Petereit, C., Hinrichsen, H.-H., Franke, A., Köster, F.W., 2014. Floating along buoyancy levels: Dispersal and survival in western Baltic fish eggs. Progress in Oceanography, 122:131-152.

Rudolph, C., Lehmann, A., 2006. A model-measurements comparison of atmospheric forcing and surface fluxes of the Baltic Sea. Oceanologia, 48(3), 333-380.

Stanley, R., Snelgrove, P. V., Gregory, R. S., 2012. Dispersal patterns, active behaviour, and flow environment during early life history of coastal cold water fishes. PloS one, 7(9), e46266.

Uzars, D., Plikshs, M., 2000. Cod (Gadus morhua L.) cannibalism in the central Baltic: Interannual variability and influence of recruit abundance and distribution. ICES Journal of Marine Science, 57(2), 324-329.

Voss, R., Hinrichsen, H.-H., St.John, M., 1999. Variations in the drift of larval cod (Gadus morhua L.) in the Baltic Sea: combining field observations and modelling. Fisheries Oceanography. 8, 199–211.

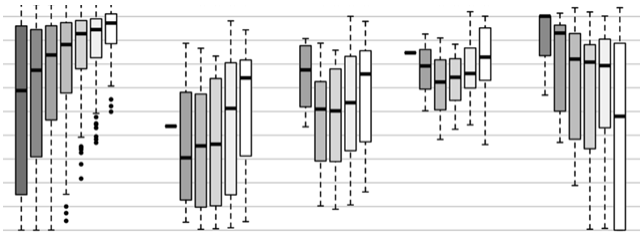
Werner F.E., Page, F.H., Lynch, D.R., Loder, J.W., Lough, R.G., Perry, R.I., Greenberg, D.A., Sinclair, M.M.,1993. Influences of mean advection and simple behavior on the distribution of cod and haddock early life stages on Georges Bank. Fisheries Oceanography 2, 43-64.

Werner, F.E., Perry, R.I., Lough, R.G., Naimie, C.E., 1996. Trophodynamics and advective influences on Georges Bank larval cod and haddock. Deep-Sea Res. II 43, 1793–1822.

Wieland, K., Waller, U., Schnack, D., 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10, 163–177.

Wieland, K., Jarre-Teichmann, A., Horbowa, K., 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science 57, 452–464.

Chapter 3



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Hindcasting the sensitivity to eutrophication of the Eastern Baltic cod (*Gadus morhua*) spawning habitat

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Abstract

Owing to the large nutrient-rich freshwater influx from its intensely farmed drainage basin, the semi-enclosed water body of the Baltic Sea is highly eutrophicated and consequently hypoxic areas have expanded 10-fold in the past century. The spawning success of Eastern Baltic cod (*Gadus morhua*) depends heavily on sufficiently oxygenated water due to its reproduction via pelagic eggs. In this study, we propose a new measure of qualifying the spawning habitat, the approach of Buoyancy Depending Reproductive Layers (BDRL). This concept provides individualized abiotic conditions for spawned eggs by the relationship between female spawner size and the depth of neutral egg buoyancy. We use this novel approach to (1) quantify the sensitivity of the habitat to eutrophication (2) reconstruct ocean acidification levels and (3) quantify a seasonal change of the spawning conditions; all in comparison with the standard approach, the Reproductive Volume (RV). To model the driving abiotic conditions, we used a mechanistic ocean model (BSIOM) with a coupled simplified oxygen sub-model, which enabled us to investigate the past development of the habitat under 3 different eutrophication scenarios between 1998 and 2015.

Both approaches showed a significant negative impact of eutrophication on the spawning habitat of cod. The level of eutrophication could therefore have a severe impact on cod reproduction success. The BDRL showed that it is especially crucial to eggs spawned by small females, which are neutrally buoyant on the deep end of the vertical distribution. The RV-approach underestimated the impact in the Bornholm Basin and Arkona Basin, and overestimated the available spawning habitat in the Gdansk Deep and Gotland Basin. The BDRL , however, identified no seasonal effects, but the inclusion of depth-resolved pH levels showed that cod eggs in the field are exposed to higher ocean acidification levels (pH low as 7.4) than used in laboratory tolerance studies. We argue that the BDRL

approach is to be favoured compared to the RV because it is more sensitive, able to incorporate stock structure, does not overestimate the spawning habitat in the eastern spawning areas and can provide estimates of other stressors or derived indicators female spawner size dependent.

Introduction

Oxygen minimum zones are expanding in many parts of the world (Stramma et al., 2010). They heavily impact community compositions of ecosystems by shrinking species' habitats and/or diminishing the quality of the habitat. Driven by the rise of ocean surface temperatures and the consequence - increased stratification - oxygen minimum zones have been building up in the open ocean over long courses of the last century and are expected to severely increase until the end of this century (Oschlies et al., 2008). Oxygen depletion in coastal areas is often accelerated by other mechanisms, e.g. a change in currents (e.g. upwelling), which can change ecosystem characteristics very rapidly (Keller et al., 2001). Coastal ecosystems are most affected by anthropogenically induced eutrophication, which increases primary production and in turn oxygen depletion. In addition, coastal areas are often characterized by higher biodiversity, species abundance and production than offshore habitats, increasing the number of species and biomass affected by deoxygenation. The Baltic Sea is highly sensitive to and affected by all factors causing oxygen depletion zones eutrophication, stratification and global warming (Carstensen et al., 2014).

A strong salinity stratification is a main feature of the Baltic Sea that prevents physical mixing of oxygen towards deeper waters even in winter (Zillén et al., 2008). Re-oxygenation in the deeper sub-basins mainly occurs through periodical advection of more saline and well-oxygenated water masses from the North Sea, the Major Baltic Inflow events (MBI; Elken and Matthäus, 2008). Between the 1950s and the 1980s increasing discharges of sewage- and waste-water caused a strong increase of nutrient loads within the Baltic Sea (Andersson et al., 2015). Since then the Baltic Sea is classified as "affected by eutrophication" (HELCOM, 2013). The consequences were increasing primary production rates in the past decades, which in turn increased the heterotrophic consumption of available oxygen below the halocline. The resulting 10-fold increase in hypoxic areas in the Baltic Sea is a textbook example for eutrophication driven expansion of oxygen minimum zones (Carstensen et al., 2014). This process is recently exacerbated by ocean warming in the Baltic Sea, reducing the oxygen solubility and further enhancing stratification along the coasts (Hinrichsen et al., 2011; Lehmann et al., 2011). Since the 1990s the yearly overall nutrient input was slowly declining (Reusch et al., 2018; HELCOM, 2017), but even under a successful nutrient reduction scenario the hypoxic areas in the Baltic Sea are unlikely to significantly decline (Meier et al., 2011), because system characteristics of the Baltic Sea are causing a retention time of nutrients of up to 50 years (Gustafsson et al., 2012b). Therefore until the continued input of nutrients is not reduced much further and then stabilized on low levels for decades, eutrophication induced stressors are likely to stay important for the Baltic Sea ecosystem.

The Eastern Baltic cod stock (*Gadus morhua)* is one of the most important commercially exploited fish stocks in the Baltic Sea and is as its role as the top predator in the system of

high ecological importance. Of the few marine fish populations in the central Baltic Sea it is one of the most impacted by the decrease of oxygen availability caused by eutrophication (e.g. Hinrichsen et al., 2016). This is because paradoxically, cod females rely on the deeper sub-basins of the Baltic Sea although these are exactly the critical areas where stratification and deep-water oxygen depletion play out. The pelagic eggs of Eastern Baltic cod need a certain water density, depending mainly on salinity, to become neutrally buoyant and avoid thereby the lethal bottom contact (Wieland, 1995). The required salinities are, however, only achieved relatively deep (>50m) in the central Baltic Sea, where oxygen conditions are often unfavorable for egg development (e.g. Hinrichsen et al., 2016). In order to characterize the available habitat for reproduction, the reproductive volume (RV) approach is an established concept to quantify the available spawning habitat for Eastern Baltic cod. To do so, the water bodies with abiotic conditions above the known physiological tolerance limits for oxygen and temperature and a minimum salinity in order for the eggs to achieve neutral buoyancy are mapped (S >11; O_2 > 2 ml/l, T > 1.5°C). This approach has been widely applied (e.g. Plikshs et al., 1993, 2015; MacKenzie et al., 2000; Margonski et al., 2010, Meier et al., 2012). Within the spawning grounds of Eastern Baltic cod in the deep sub-basins of Bornholm, Gdansk and Gotland, environmental spawning conditions were thereby unsurprisingly identified to be negatively impacted by the deoxygenation process in the recent decades.

Yet this approach has limitations, in particular because egg buoyancy varies markedly between individual fish (Nissling & Westin, 1991) and is positively correlated to egg diameter, while the diameter of eggs in turn is strongly dependent on size and age of the female spawning the eggs (Valling & Nissling 2000). Given that the size and quality of cod eggs and hence, their buoyancy, critically depend upon female size the spawned eggs of small females have to develop possibly further down in the water column than the eggs spawned by larger females. The strong stratification of the Baltic Sea sub-basins, also in terms of oxygen, could then result in a severe difference in reproductive chances for different sized fish. Here the RV approach is not able to differentiate and gives also no information of the relative quality of the habitat, but gives only the volume of the water body which is meeting the minimal requirements (see also Vallin and Nissling, 2000, their Figure 2). Therefore to incorporate the mechanisms relevant for egg buoyancy, we here apply a novel individualized approach, taking into account the estimated vertical extent of neutral buoyancy in the water column of eggs spawned by individualized fish along with the projected habitat conditions on that water layer, the approach of Buoyancy Dependent Reproductive Layers (BDRL). Our intention was to approximate the impact of the size-depending mechanisms and also to compare the individualized approach with older assessments that only consider the reproductive volume and therefore use only one overall minimum salinity requirement, given that the size of spawners decreased dramatically in recent years.

With the BDRL approach not only the spawner size specific oxygen dependent survival chances of the spawned eggs (Köster et al., 2005) can be assessed but also other possible stressor associated with hypoxic conditions within the spawning grounds. The RV approach would here only yield parameters that are integrated over a large heterogenic water body. First feeding larvae of Eastern Baltic, for example, have to perform a vertical

migration from the layers of neutral buoyancy up to the euphoticzone in order to feed visually on zooplankton prey (Grønkjær et al., 1997; Grønkjær and Wieland 1997, Huwer et al., 2011). This migration has to be performed by active swimming because pre-metamorphic larvae do not possess a swim bladder yet. The active swimming behavior or larval vertical migration activity (Y_{LVMA}) is oxygen dependent (Rohlf, 1999). Because newly hatched larvae do remain approximately at depths they hatch until the migration (Huwer et al., 2011), Y_{LVMA} can be assessed by the BDRL approach individually. Another possible stressor that can be assessed is the prevailing level of pH during egg development. Caused by heterotrophic degradation of organic material and the associated increase of the metabolic waste product CO_2, the prevailing pH in hypoxic areas in the Baltic Sea can reach values far below expected future levels for the open ocean surface (Melzner et al., 2012). This study holds the chance of an detailed assessment of the ranges of oxygen and pH being already experienced by Eastern Baltic cod early life stages and could be used as reference point for future studies on physical tolerance levels.

In order to assess the cod habitat available to reproduction with both approaches we used a high resolution hydrodynamic model for the entire Baltic Sea (BSIOM) to hindcast monthly property fields of salinity, temperature and oxygen. The mechanistic ocean model uses realistic atmospheric forcing that is based on observations available only in the hindcast mode. Hindcast models possess besides the advantage of more realistic forcing the ability to be altered in only one parameter, which is ideal for habitat sensitivity studies. We calculated sub-basin specific time series of the reproductive volume, as well as the abiotic conditions on individualized levels of neutral egg buoyancy. Three model runs were performed for the time interval 1998 to 2015 simulating 3 different eutrophication scenarios: a linear 30% increase, the real world time course with constant eutrophication levels, and a linear decrease of 30%. In this way, not only the recent development of the spawning habitat of Eastern Baltic cod could be assessed and compared between BDRL and RV approach, but also the sensitivity of the system towards shifts in eutrophication could be investigated.

Our objective was to (i) examine the sensitivity of cod reproductive habitat to eutrophication (ii) further establish the novel BDRL approach that considers female size and hence, egg buoyancy for examining the reproductive habitat and success (iii) compare the established reproductive volume approach with the BDRL approach and (iv) use this approach to approximate experienced acidification levels by eggs and larvae.

Materials and Methods

Oceanographic modeling

To simulate eutrophication scenarios in hindcast and to provide a synoptic data source for the hydrographic conditions within the distribution area of Eastern Baltic cod, an established ocean model framework was used - The Kiel Baltic Sea Ice-Ocean Model (BSIOM; Lehmann, 1995; Lehmann & Hinrichsen, 2000; Lehmann et al., 2002). Its horizontal resolution was 2.5 km and consisted in the vertical of 60 levels. The model domain included the Baltic Sea, Kattegat and Skagerrak. It was complemented by an

oxygen consumption sub-model producing oxygen property fields for the entire Baltic Sea at the same resolution (Lehmann et al., 2014). It uses idealized primary production levels represented as a factor in the oxygen tracer to calculate depletion rates on the 3D model grid points. In order to force the hydrographical model a realistic atmospheric forcing was chosen with the ERA-Interim reanalysis fields (Dee et al., 2011). These are available at a temporal resolution of 6 hours and were downloaded on a regular grid of 0.5°x 0.5°. Forcing data were interpolated and included surface air pressure, precipitation, cloudiness, and air- and dew point temperatures at 2m height. Wind speed and direction at 10 m height were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast (Bumke et al., 1998). BSIOM forcing functions, such as wind stress, radiation and heat fluxes were calculated according to Rudolph and Lehmann (2006). Additionally, river runoff was prescribed from a monthly mean runoff data set (Kronsell & Andersson, 2012).

Following a pre-experimental stabilization period of 25 years the model setup was run under three different eutrophication scenarios for the period 1998 to 2015. The runs included a "best guess"-scenario following the real world time course with constant eutrophication levels (Andersen et al., 2017; HELCOM, 2017) and two experimental runs simulating a decrease and increase of eutrophication by 30%, respectively. Developments in the eutrophication level were realized by means of the primary production factor in the oxygen sub-model. For the stabilization period it was additively increased from 0.5 to 1 by a factor of 0.018 per year - following the idealized development of the total Baltic Sea primary production for this time period: An increase from 34.85 x 10^6 t C yr^{-1} in 1970 (Keiser et al., 1981) to 62 x 10^6 t C yr^{-1} in 2000 (Wasmund et al., 2001). Subsequently, beginning from the 1st of January 1998 until the end of 2015, the factor was first kept constant at 1 for the "best guess"-scenario and was then in the two following runs set to continuously increase and decrease by 0.018 per year to the final levels of 1.333 and 0.667 in 2015, respectively. Thereby we (i) extended the increase of primary production during stabilization to a final total production of about 80 x 10^6 t C yr^{-1} in 2015 (increase of 30%) and (ii) simulated also the inverted scenario, in which the primary production decreases again after acclimatization on the inverted rate to about 44 x 10^6 t C yr^{-1} in 2015 (decrease of 30%). The changing rates were explicitly chosen to simulate a realistic development in the eutrophication level within the mechanistic- and oxygen sub-model. Daily values of the parameters salinity, temperature and oxygen were compiled and temporally interpolated to a monthly resolution for further analyses.

Habitat modeling

To characterize the habitat quality for cod reproduction, time series in monthly resolution of abiotic- and derived parameters on neutral egg buoyancy levels (BDRL approach), as well as the reproductive volume (RV) were compiled. To factor in the bathymetric structure of the Baltic Sea calculations were done sub-basin specific, for which horizontal constrains were chosen that represent adapted ICES Subdivisions (Figure 1) Modeling was performed with R (R Development Core Team, 2011) and Fortran (GFortran, 2011) on the compiled data of the hydrographical model runs.

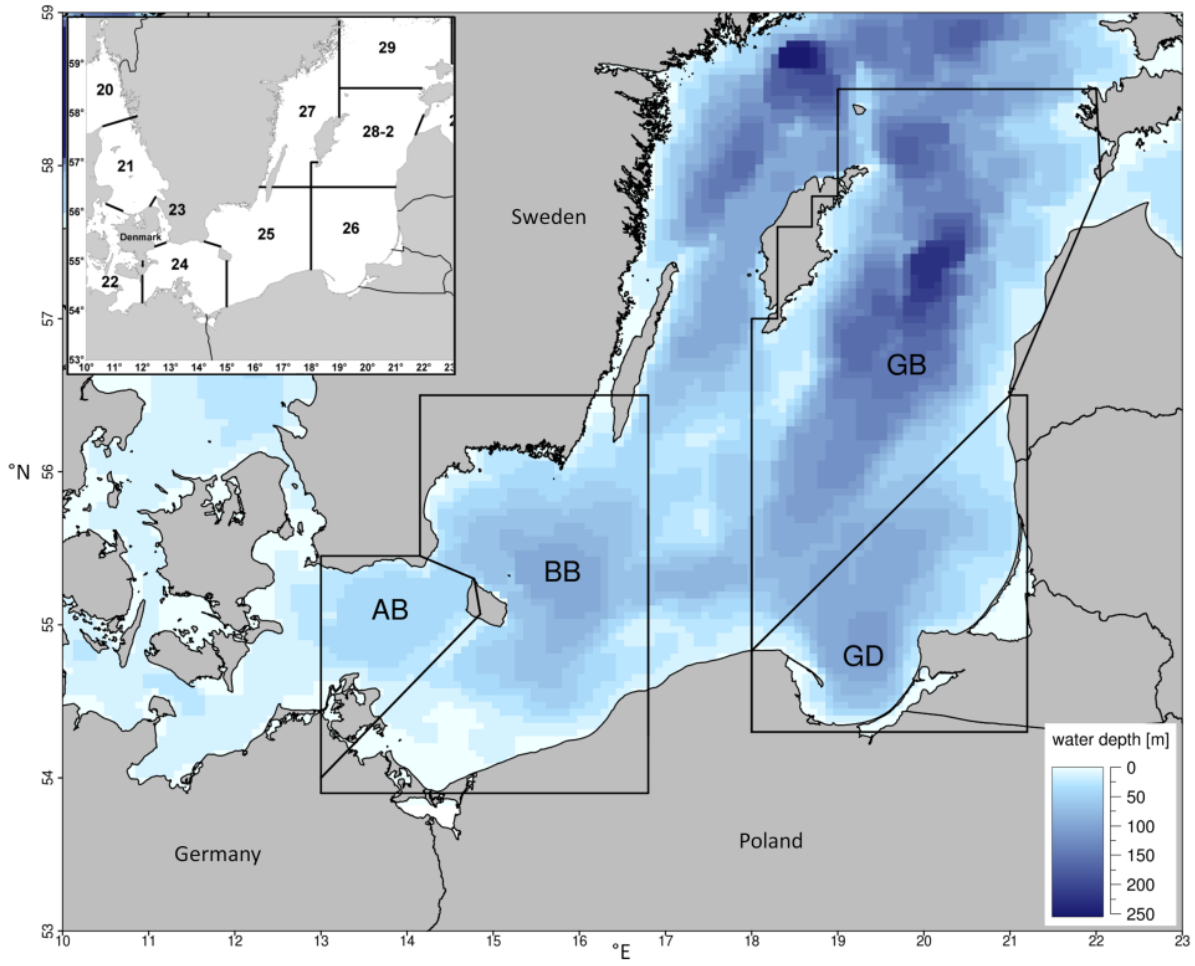

Figure 1: Map of the Baltic Proper with the horizontal borders of adapted ICES rectangles used as sub-basin representations. AB= Arkona Basin; BB=Bornholm Basin; GD=Gdansk Deep; GB=Gotland Basin. Inlet shows the split of the area by the original ICES subdivisions.

The BDRL approach was to investigate the characteristics of the reproductive habitat by the means of the conditions found on several specific layers of water density. The layers represent mean neutral egg buoyancies of eggs spawned by females of 7 staggered size classes, and are based on the findings of Vallin and Nissling (2000), who incorporated own measurements with all data and literature available to them to build a model which is using female size to predict egg buoyancy. The here reported female size specific temperatures and salinities of neutral egg buoyancy were converted after Millero and Kremling (1976) into mean water density levels. The results are shown in Table 1 and were used in the following to assess the available horizontal expansion of- and the prevailing abiotic conditions at the layer of water density where eggs can achieve neutral buoyancy. The assessed conditions included the mean oxygen content, as well as the oxygen derived parameters pH, egg survival probability (Y_{surv}) and larval vertical migration activity (Y_{LVMA}).

Table 1: Mean water density levels of neutral egg buoyancy for eggs spawned by different size/length classes of female spawners of Eastern Baltic Cod derived from results from Vallin and Nissling (2000). Shown is also the approximate age of the size class and the approximated salinity associated with the water density level within the common temperature range of the Baltic Sea.

length class [cm]	Approximate age [years]	Water density [kg/m^3 - 1t]	Approximate salinity range
21-37	2	12.71	15.4 – 16.1
38-49	3	12.06	14.9 – 15.6
50-60	4	11.61	14.3 – 15.0
61-69	5	11.25	13.8 – 14.6
70-76	6	10.91	13.4 – 14.2
77-83	7	10.71	13.1 – 13.9
>84	8+	10.21	12.5 – 13.2

In order to transport the BDRL concept to the hydrographical model output it was complemented at full resolution by using the appropriate calculations with the following parameters: water density, oxygen saturation, vertical larval migration activity (Y_{LVMA}) and oxygen depending egg survival (Y_{surv}). R routines within the packages marelac (Soetaert et al., 2012) and oce (Kelley, 2011) were used for calculating water density and oxygen saturation, respectively. The equation for Y_{surv} is derived from experimental data and was taken from Köster et al. (2005):

$$y_{surv} = 100((1 - e^{-0.71x})^{11.63}), \quad (1)$$

where y_{surv} is the oxygen depending survival before hatch (%) and x the oxygen content in ml l^{-1}. The function describes a sigmoid curve with a <4 % survival chance at oxygen levels below 2 ml l^{-1}, a 50% chance of survival at 4 ml l^{-1} and more than 90% chances at oxygen levels above 6.7 ml l^{-1}.

Y_{LVMA} was calculated with a formula adapted after experimental data from Rohlf (1999).The equation gives percentage values of vertical swimming activity of first feeding larvae depending on the available oxygen content:

$$y_{LVMA} = -28 + 2.3979x - 0.0141x^2, \quad (2)$$

where y_{LVMA} is the vertical swimming activity (%) and x the oxygen saturation. The function describes a polynomial curve of second degree with no vertical swimming activity till 13% of oxygen saturation, about 50% activity at ~44% oxygen saturation and 75% activity at 85% oxygen saturation.

To complement the model responses with ocean acidification levels, linear relationships between the oxygen concentration and pH within in situ measurements were applied to oxygen concentrations given by the model output. The ICES Oceanographic data base was chosen as data source (ICES, 2009) to produce the relationships. All available data of the last 40 years for oxygen and pH within sub-basin specific depths, representing conditions

below and within the permanent halocline, was downloaded and compiled in a monthly resolution. Here again the adapted ICES subdivisions were used as horizontal sub-basin specifications (Figure 1). The identified strongly linear relationships between the prevailing oxygen conditions and the corresponding pH (Table S5) were then applied to the oxygen data output from the ocean model in a depth dependent manner, resulting in a full pH data set for the depths relevant for Eastern Baltic cod reproduction.

Lastly all compiled data was vertically interpolated in relation to water density to be able to select all data values on the specific layers of water density (Table 1). With that sub-basin-specific time series of monthly means could be compiled that characterize the cod spawning habitat female size-dependent by the means of the horizontal expansion as well as the oxygen dependent quality of the water density layer where spawned eggs achieve neutral buoyancy.

The findings of the BDRL approach were compared with results obtained from the classical RV approach. The RV is defined according to MacKenzie et al. (2000) as the volume of water bodies within the sub-basins with S>11, O_2>2ml/l and T>1.5°C. For each horizontal grid point of the model data the vertical extension of the RV was calculated which then could be scaled up into sub-basin-specific monthly time series.

Statistical analyses

All data sets were analyzed with generalized linear models (GLM) using the SAS university edition software. Significance was taken at $p<0.05$ for all tests. Post hoc test techniques were chosen depending on the data balance as Tukey (after Tukey, 1953) for data sets representing balanced designs or Scheffé (Scheffé, 1959) for unbalanced designs. The resulting models resembled ANCOVA-type tests that used time as covariate and various combinations of the factors sub-basin, eutrophication scenario and female size as main, controlling, or interacting effects depending on the data set and/or the investigative question. For the analysis only data within the spawning season was considered (March - August). The impact of eutrophication was tested by choosing the eutrophication scenarios as main factor while controlling for sub-basin and female size, whereas the sub-basin effect was tested by using sub-basin as main effect while controlling for the eutrophication scenario and female size. A possible seasonal component within the effects was assessed by introducing a new grouping factor of spawning time with March to May (early spawning time) and June to August (late spawning time) as factor levels. These were orientated on the historical spawning times and the shift of peak spawning activity (Wieland et al., 2000; Baranova et al., 2011; Köster et al., 2016). This factor was then used as main effect variable in the statistical model replacing the covariate time.

Separate GLMs were fitted to the data sets produced by the BDRL-approach to characterize the cod spawning conditions by the conditions found on specific layers of water density. The response parameters were (i) horizontal expansion, (ii) depth, (iii) oxygen, (iii) y_{surv}, (iv) y_{LVMA} and (v) pH of/on the layers of water density. For comparison analogue analyses were made with the (vi) RV data set, in which the factors of the models were used in the identical way, minus the factor of female size. The parameters of horizontal expansion and depth of the layer of water density were not influenced by the

BSIOM oxygen sub-model and were hence analyzed only for one eutrophication scenario. They exhibited significant correlations and were therefore firstly tested with a MANCOVA-type approach for overall significance before they could be analyzed in more depth by univariate tests. The response parameter oxygen and the oxygen derived parameter characterizing the quality of the spawning habitat were tested separately in univariate tests for the impact by sub-basin, eutrophication scenario and female size as well as the interactions of sub-basin and eutrophication scenario and the 3-way interaction of sub-basin, eutrophication scenario and females size. Within the eastern basins some female size classes were for significance tests excluded, when there were less than 10 data points available.

Results

The BDRL approach is using female spawner size depending neutral egg buoyancies to assess the spawning habitat of Eastern Baltic cod. The size of the habitat is herein defined as the horizontal expansion of the water density layers of neutral egg buoyancy. We calculated and compared these horizontal expansions between the Baltic Sea sub-basins and identified the Bornholm Basin (BB) followed by the Arkona Basin (AB) as the most substantial spawning habitat within the period 1998 to 2015 (Figure 2). These two basins combined represented up to 33fold larger horizontal expansions of suitable water density layers than the eastern sub-basins Gdansk Deep (GD) and Gotland Basin (GB). Here, eggs spawned by females <60 cm were extremely seldom able to be buoyant in the water column and larger females only found suitable salinities shortly after the two MBIs in 2003 and 2014/2015 (Figure 2, Figure 6).

The horizontal expansion of suitable water density layers averaged over all basins was found to significantly increase with female spawner size (Figure 2). The available habitat increased by about 22% per size class from a mean of 1167 km^2 for the smallest size class to 3731 km^2 for the largest size class. Evidently, this effect is a direct consequence of larger and more buoyant eggs spawned by larger females, which will float in less saline water layers higher in the water column compared to those from small females. Taken together this increases the size of the suitable part of the stratified sub-basin. The vertical depth of water layers displaying neutral egg buoyancy were therefore distributed within and below the sub-basins position of the permanent halocline (Figure 2). We identified marked effects of spawner size and sub-basin. The strongest decrease in depth of neutral egg buoyancy with size class was found in the BB (2.6 m per size class), while there was only a weak difference among the length classes in their capability to produce eggs that float higher in other sub-basins. Additionally we found within the GB the reversed behavior for eggs of the largest spawner size class (>84 cm) caused by special circumstances. The exceptional Major Baltic Inflow (MBI) event in 2003 provided substantial amounts of saline water masses to the GB and produced suitable water density layers for the largest spawner size class for several years. However, because it lasted until 2014 for another MBI, water in the GB became less saline so that the suitable water density layer gradually sank to depths irrelevant for cod reproduction.

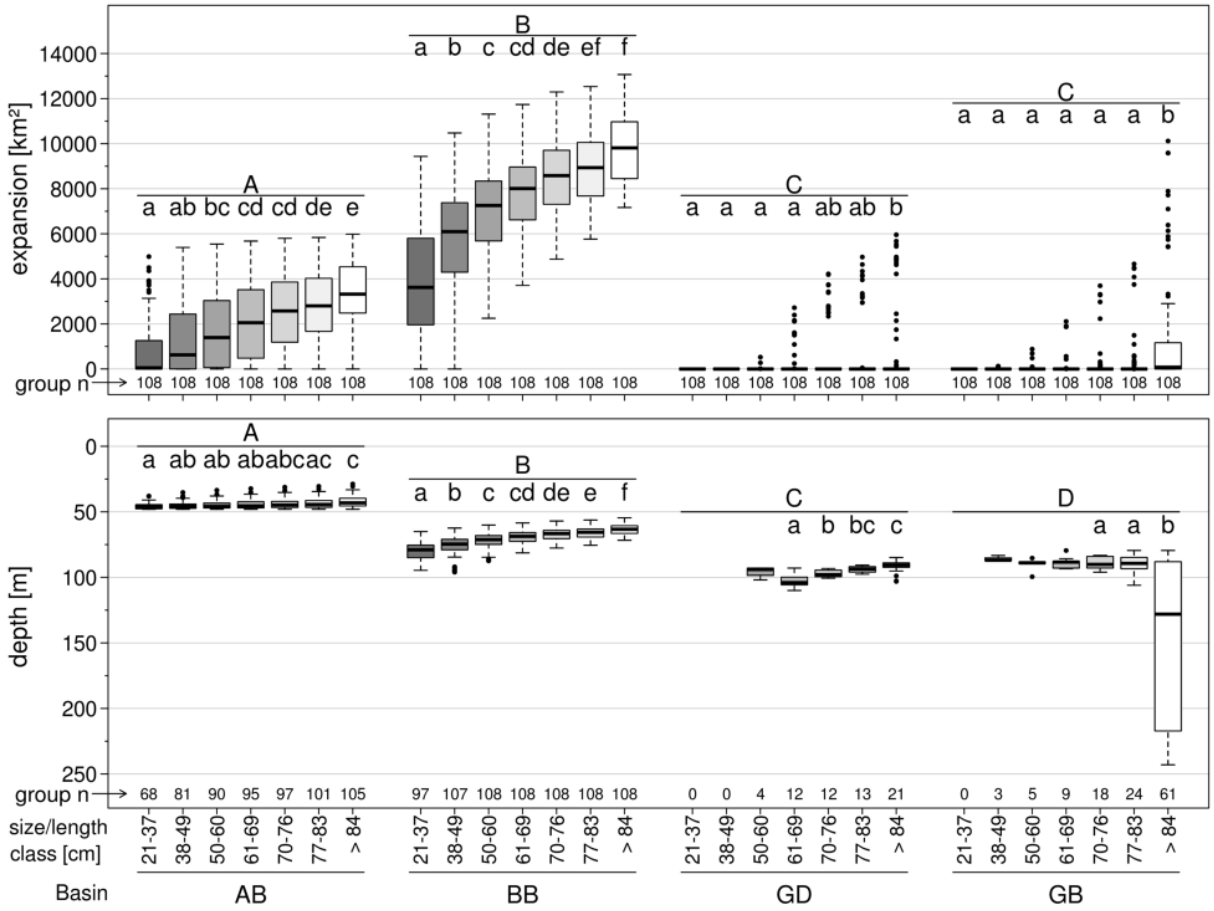

Figure 2: Horizontal area expansion (top panel) and mean depth (bottom panel) of water density layers of neutral egg buoyancy of Eastern Baltic cod within the spawning seasons 1998 to 2015. Data is organized into 2 levels of groups: sub-basins (AB: Arkona Basin, BB: Bornholm Basin, GD: Gdansk Deep, GB: Gotland Basin) and size classes of female spawners. Significant differences are depicted for sub-basins in capital letters and for size classes of female spawners in small letters.

Oxygen conditions within the water density layers of neutral egg buoyancy were found to be negatively correlated with depth (Table 2). Best oxygen conditions for developing eggs were found therefore for the AB where suitable water layers were found between 28 and 48 m deep and rarely showed levels below 5 ml/l O_2. The BB showed a wider range of oxygen conditions between hypoxic levels and above 7 ml/l O_2, found in the depth of suitable water layers between 54 and 96 m. The eastern sub-basins GD and GB showed poor and rapidly deteriorating oxygen conditions following the two MBIs in 2003 and 2014/2015 (Figure 3, Figure 6). Within the BB and GB we found a significant effect of female spawner size on the oxygen conditions experienced by eggs that differed among sub-basins (Figure 3, Table S1). Within the BB the spawner size had a positive effect on oxygen levels (+0.32 ml/l O_2 per size class) while in the GB eggs of the largest spawner size group would experience lower oxygen conditions than all smaller classes. This is, however, caused by the exceptional period following the strong MBI in 2003 and cannot be seen as a general trend, also because there were only very few data points available to compare this result to the smaller spawner size classes.

Table 2: Coefficients and statistics of the dependency of the oxygen content [ml/l] in layers of water density on their depth [m] in the water column. Shown are sub-basin- and eutrophication-scenario-specific regression results (AB= Arkona Basin, BB= Bornholm Basin, GD= Gdansk Deep and GB = Gotland Basin).

Basin	Eutrophication scenario	y_0	slope	R sqr.	adj. R sqr.	st. error	F	Df. Resid.	p
AB	30% increase	13.18	-0.145	0.20	0.20	1.078	163.3	638	<.0001
	constant	12.99	-0.137	0.20	0.20	0.993	164.9	635	<.0001
	30% decrease	12.32	-0.119	0.18	0.18	0.929	146.2	638	<.0001
BB	30% increase	16.14	-0.162	0.52	0.52	1.154	799.5	740	<.0001
	constant	16.11	-0.156	0.49	0.49	1.161	717.7	742	<.0001
	30% decrease	15.79	-0.147	0.47	0.47	1.152	664.2	740	<.0001
GD	30% increase	5.84	-0.021	0.01	0.01	1.337	0.62	68	0.43
	constant	8.27	-0.041	0.05	0.03	1.066	3.05	60	0.085
	30% decrease	4.94	0.0001	0.00	-0.01	0.836	0.00	68	0.99
GB	30% increase	8.18	-0.036	0.71	0.71	1.197	296.2	122	<.0001
	constant	8.72	-0.038	0.79	0.79	1.021	451.0	118	<.0001
	30% decrease	9.27	-0.039	0.84	0.84	0.898	629.4	122	<.0001

With the BDRL-approach we are able to assess the impact of past eutrophication scenarios on the available oxygen content on the water density levels, which then translates to direct survival chances of spawned eggs (y_{surv}), experienced acidification levels (pH) and the vertical swimming activity of hatched larvae to migrate upwards to feeding depths (y_{LVMA}) (Figure 3, Figure 4). A simulated 30% eutrophication decrease or increase changed all parameters significantly within all sub-basins, with the exception of y_{LVMA} in the GB (Table 3). The impact of eutrophication was however found to be sub-basin dependent, resulting in a significant interaction effect of sub-basin and eutrophication scenario. The largest impact was found for the GD resulting in a mean difference between the tested scenarios with respect to oxygen conditions of 1.28 ml/l, which translates into differences in acidification of pH 0.1, increased egg survival chances by 25.1% and larval migration activity by 18%. The impact of eutrophication on conditions in BB and GB were found to be at about half of the strength as found for the GD. Although statistically significant (Table S4) the impact of eutrophication on abiotic conditions was only small in the AB (deltas: O2 = 0.3 ml/l; pH = 0.02; y_{surv} = 3 %; y_{LVMA}= 0.5 %).

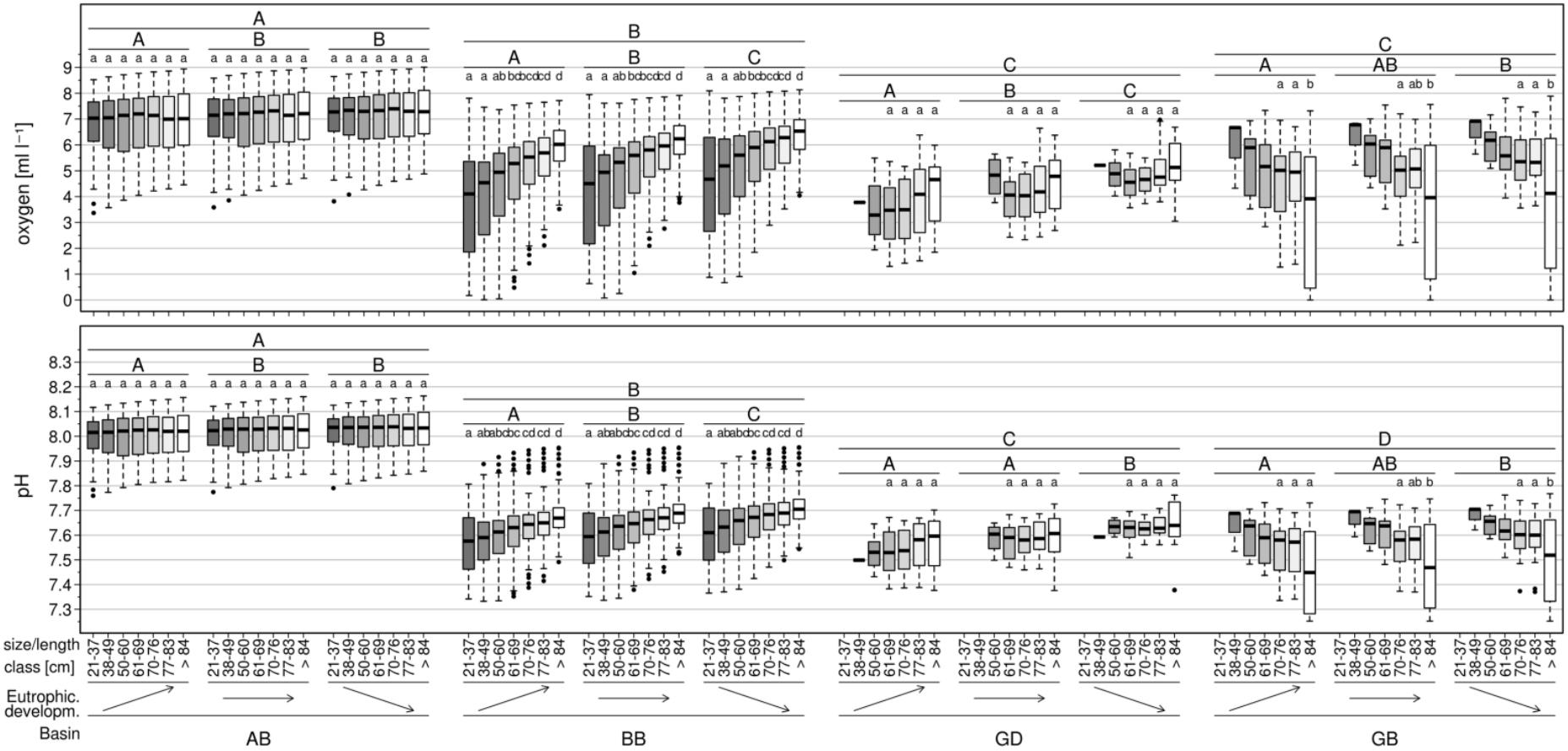

Figure 3: Oxygen (top panel) and oxygen derived pH (bottom panel) on water density levels of neutral egg buoyancy within the spawning seasons 1998 to 2015. Data is organized into 3 levels of groups: sub-basins (AB: Arkona Basin, BB: Bornholm Basin, GD: Gdansk Deep, GB: Gotland Basin), eutrophication scenarios (30% increase, constant, 30% decrease) and size classes of female spawners (Table 1). Significant differences are depicted for sub-basins and eutrophication scenarios in capital letters and for size classes of female spawners in small letters.

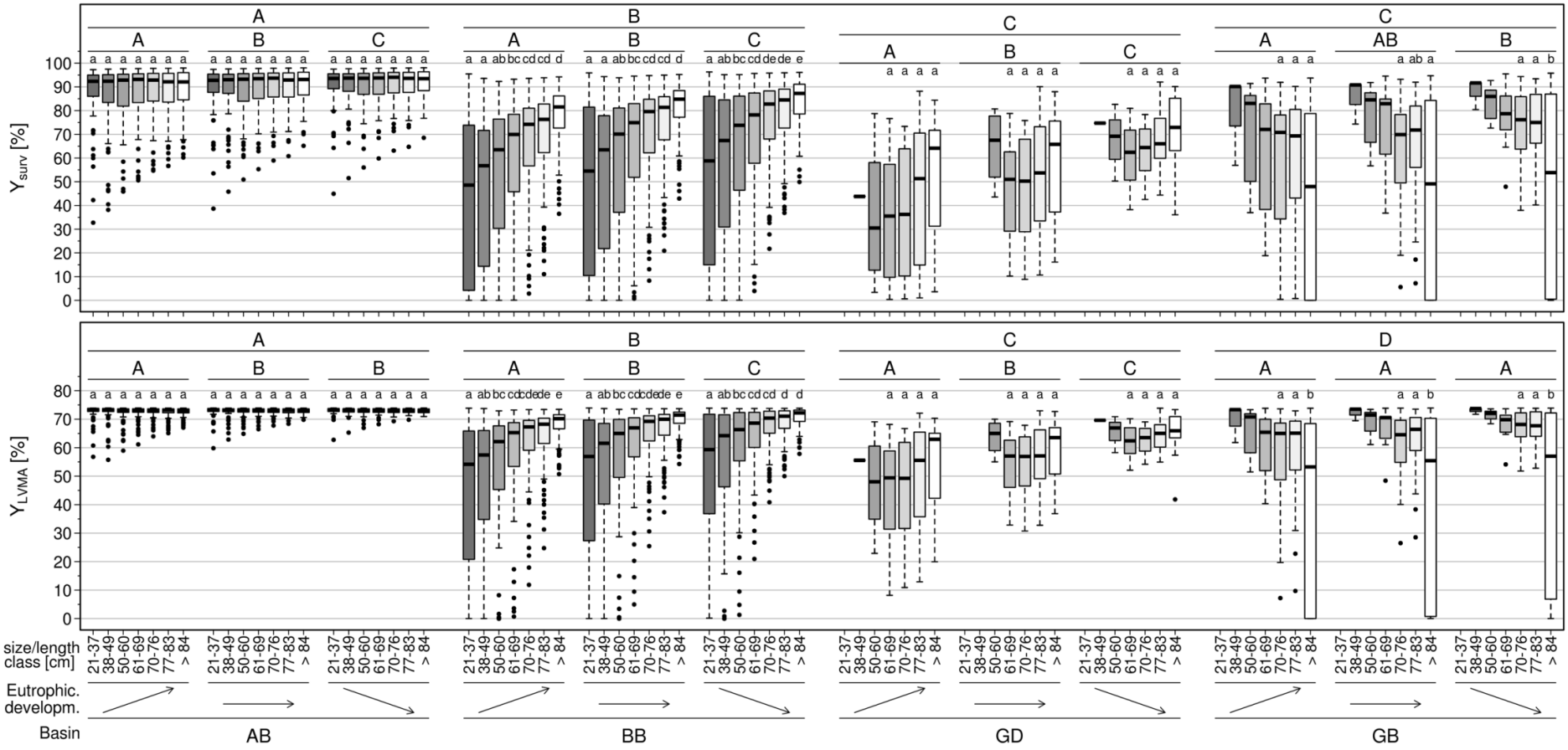

Figure 4: Oxygen depending egg survival (Y_{surv}; top panel) and larval vertical migration activity (Y_{LVMA}; bottom panel) on water density levels of neutral egg buoyancy within the spawning seasons 1998 to 2015. Data is organized into 3 levels of groups: sub-basins (AB: Arkona Basin, BB: Bornholm Basin, GD: Gdansk Deep, GB: Gotland Basin), eutrophication scenarios (30% increase, constant, 30% decrease) and size classes of female spawners (Table 1). Significant differences are depicted for sub-basins and eutrophication scenarios in capital letters and for size classes of female spawners in small letters.

Table 3: Statistical analysis of the impact of sub-basin and eutrophication scenario on the oxygen content and oxygen derived parameters (pH, y_{surv}, y_{LVMA}) on water density layers of neutral egg buoyancy. Results for effects within specific sub-basins are indicated by the column 'basins included' (all=All Basins included, AB=Arkona Basin, BB=Bornholm Basin, GD=Gdansk Deep, GB=Gotland Basin).

Response parameter	Basins included	Effect parameter	Controlled parameter	F-Value	DF model	DF Error	p value
	All	Sub-basin	Eutrophication scenario, female size class and time				
O_2				812.91	3	4696	<.0001
pH				5866.40	3	4696	<.0001
Y_{surv}				661.83	3	4696	<.0001
Y_{LVMA}				458.80	3	4696	<.0001
		Interaction Sub-basin * Eutrophication scenario	Eutrophication scenario, sub-basin, female size class and time				
O_2				2.90	6	4696	0.008
pH				2.38	6	4696	0.027
Y_{surv}				6.52	6	4696	<.0001
Y_{LVMA}				8.90	6	4696	<.0001
		3-way interaction Sub-basin*Eutroph. Scenario and size class	Eutrophication scenario, sub-basin, female size class and time				
O_2				6.27	65	4637	<.0001
pH				4.54	65	4637	<.0001
Y_{surv}				8.12	65	4637	<.0001
Y_{LVMA}				11.23	65	4637	<.0001
		Eutrophication scenario	female size class and time				
O_2	AB			12.22	2	1907	<.0001
	BB			39.62	2	2218	<.0001
	GD			23.99	2	193	<.0001
	GB			3.59	2	359	0.0287
pH	AB			12.18	2	1907	<.0001
	BB			27.03	2	2218	<.0001
	GD			18.64	2	193	<.0001
	GB			3.28	2	359	0.0389
Y_{surv}	AB			16.57	2	1907	<.0001
	BB			30.84	2	2218	<.0001
	GD			28.20	2	193	<.0001
	GB			3.99	2	359	0.0193
Y_{LVMA}	AB			16.14	2	1907	<.0001
	BB			28.39	2	2218	<.0001
	GD			31.02	2	193	<.0001
	GB			2.99	2	359	0.0515

The impact of eutrophication on cod spawning habitat quality was found to be different not only among sub-basins but also among spawner size classes, i.e. certain females sizes reacted more strongly to increase or decrease of past eutrophication depending on basin, hence resulting in a statistical 3-way interaction (Table 3). Within the BB and GB oxygen conditions for eggs of smaller females were significantly stronger negatively impacted than those for larger females (Table S1; S5). Note that these impact differences were found for pooled data of the eutrophication scenarios of all spawning seasons between 1998 and 2015. Within this period the eutrophication scenarios diverged only gradually from one

another from the same starting point. The reactions to the scenarios in the pooled data among the spawner size classes in oxygen conditions for eggs were therefore found to be small (from 0.19 ml/l in the BB to 0.42 ml/l in the GB).

To compare these findings to the "classical" approach we calculated also the RV for all sub-basins and eutrophication scenarios (Figure 5). The BB RV was largest, (199.47 km^3) followed by GB (71.25 km^3), AB (53.37 km^3) and the GD (42.71 km^3) (all means different from one another). Only the decreasing eutrophication scenario enlarged RV averaged across basins (Table 4). In a basin specific analysis we identified the RV to be impacted by eutrophication only in the GB and BB, whereas the results for the AB and GD were not significant. The eutrophication scenarios had a significant effect (Table 4) on the RV in the GB, with decreasing eutrophication producing a significantly larger RV. The BB was impacted within stagnation periods characterized by low salinity and oxygen content in the system. During these periods RV calculations for the GB and GD were tending to 0, whereas the RV in the BB was found to be around 150 km^3. To test the impact of eutrophication on the RV of the BB selectively for these periods, we empirically tested a threshold in the statistical test, where only data falling below this threshold were included in the analysis and found the critical level to be 205 km^3. When the RV within the BB falls below this threshold, the impact became significant (Figure 5). When all data was included the RV within the BB was not impacted. This shows that from the perspective of the RV approach the BB is only significantly impacted by eutrophication during stagnation periods, while the impact is shifted to the GB during situations of regular MBIs. When these findings are compared to the BDRL approach, the RV approach shows only a negative impact of eutrophication within one sub-basin at a time, while the BDRL approach identified all sub-basins to be impacted.

By the means of the RV calculations for the last two years of the modeled period (2014 and 2015) the largest potential for an expanding spawning habitat was identified for the GB. An exceptionally large MBI in December 2014 resulted into an increase of RV for the constant eutrophication scenario from very low levels to 265 km^3. The potential was further amplified under the scenario of a decrease of eutrophication by 30% to very large 733 km^3 RV within 2015. Although the MBI was also triggering larger RVs in all other sub-basins, the eutrophication scenarios did here not significantly differ. We were not able to identify this behavior with the BDRL approach. Here no exceptional impact by the inflow specifically on the GB environment was found. The increase of salinity in the GB caused by this event was not sufficient to sustain neutral egg buoyancy for the large majority of size classes, but satisfied the salinity requirement for the RV of 11 PSU.

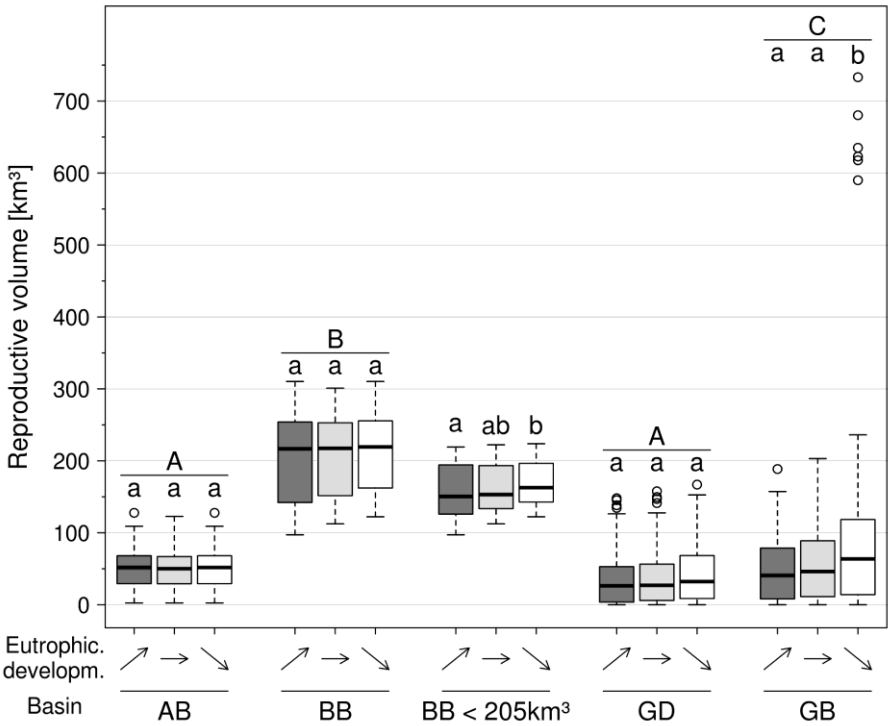

Figure 5: Reproductive volume (RV) of Eastern Baltic cod within the spawning seasons 1998 to 2015. Data is organized into 2 levels of groups: sub-basins (AB: Arkona Basin, BB: Bornholm Basin, GD: Gdansk Deep, GB: Gotland Basin) and eutrophication scenarios (30% increase, constant, 30% decrease). Significant differences are depicted for sub-basins in capital letters and for eutrophication scenarios in small letters. Additionally outside of the basins comparison, the result for a reduced data set of the Bornholm Basin is shown where only monthly means < 205 km^3 were included.

A direct comparison between the RV and the BDRL approach is difficult, since the RV is a combined measure of habitat size and quality, while the BDRLs yield separate measures of habitat size and quality for 7 different spawner size classes. We therefore used a mean horizontal expansion of all 7 size classes and compared it with the RV in their timely development relative to an overall mean of each parameter in the constant eutrophication scenario (Figure 6). The RV approach clearly suggested that the GD and GB provide regularly suitable spawning habitats in a substantial size, whereas the BDRL approach identified here only small windows of several months as suitable for the eggs spawned by most spawner size classes to find neutral buoyancy within the water column. For the AB and BB on the other hand both approaches showed comparable timely coverage and relative size variations in spawning habitat between 1998 and 2015. Compared to the overall mean of the parameters, however, the BDRL rates the size of the available habitat here consistently higher.

Table 4: Statistical analysis of the impact of sub-basin and eutrophication scenario on the Reproductive Volume of Eastern Baltic cod. Results for effects within specific sub-basins are indicated by the column 'basins included' (all=All Basins included, AB=Arkona Basin, BB=Bornholm Basin, GD=Gdansk Deep, GB=Gotland Basin). For all tests time was used as covariate. For the sub-basin effect it was additionally controlled for eutrophication scenario.

Basins included	Effect parameter	Controlled parameter	F-Value	DF		p value
					error	
All	Sub-basin	- Eutrophication scenario - time	580.11	3	1283	<.0001
All	Interaction sub-basin * Eutrophication scenario	- sub-basin - Eutrophication scenario - time	4.77	6	1283	<.0001
	Eutrophication scenario	time				
AB			0.03	2	320	0.969
BB			0.61	2	320	0.546
GD			0.67	2	320	0.514
GB			9.69	2	320	<.0001

Regardless which approach is used, one possible application of habitat quality mapping for Eastern Baltic cod is to check whether the observed change in peak spawning activity is influencing the encountered abiotic conditions during spawning activities. Therefore we assessed the seasonal development of the abiotic conditions in the spawning habitat and the sensibility of this seasonal component to changes in eutrophication. A significant negative development of conditions during the spawning time between the time windows March - May (early) and June - August (late) averaged over all sub-basins was detected by both approaches. The overall mean oxygen conditions on egg buoyancy levels decreased by 1.0 ml/l and the RV decreased by 7.2 km^3. A sub-basin specific test however showed that the RV had a seasonal component only within the GB, while assessed by the BDRLs, oxygen and all dependent quality parameters on egg buoyancy levels changed significantly within the spawning season in all other sub-basins (Table S3). The eutrophication level impacted this seasonal development not significantly.

As another improvement the BDRL approach allows us to include the acidification levels that are experienced by cod eggs during development. For this purpose we used decadal sub-basin specific correlations between in-situ measurements of pH and oxygen (Table S6) and applied these to the oxygen conditions found on the water density layers of neutral egg buoyancy (Figure 3). The approach identified major differences among all sub-basins. Within the AB pH values around 8 and a variance of about 0.4 units were found on the egg buoyancy levels of all female spawner size classes, whereas within the BB a wide range of low pH values from 7.3 to 7.9 were observed with significant higher values experienced by eggs spawned by larger female spawners. The impact by eutrophication was found to be significant within all basins, but resulted only in minor changes of pH of about 0.1 units.

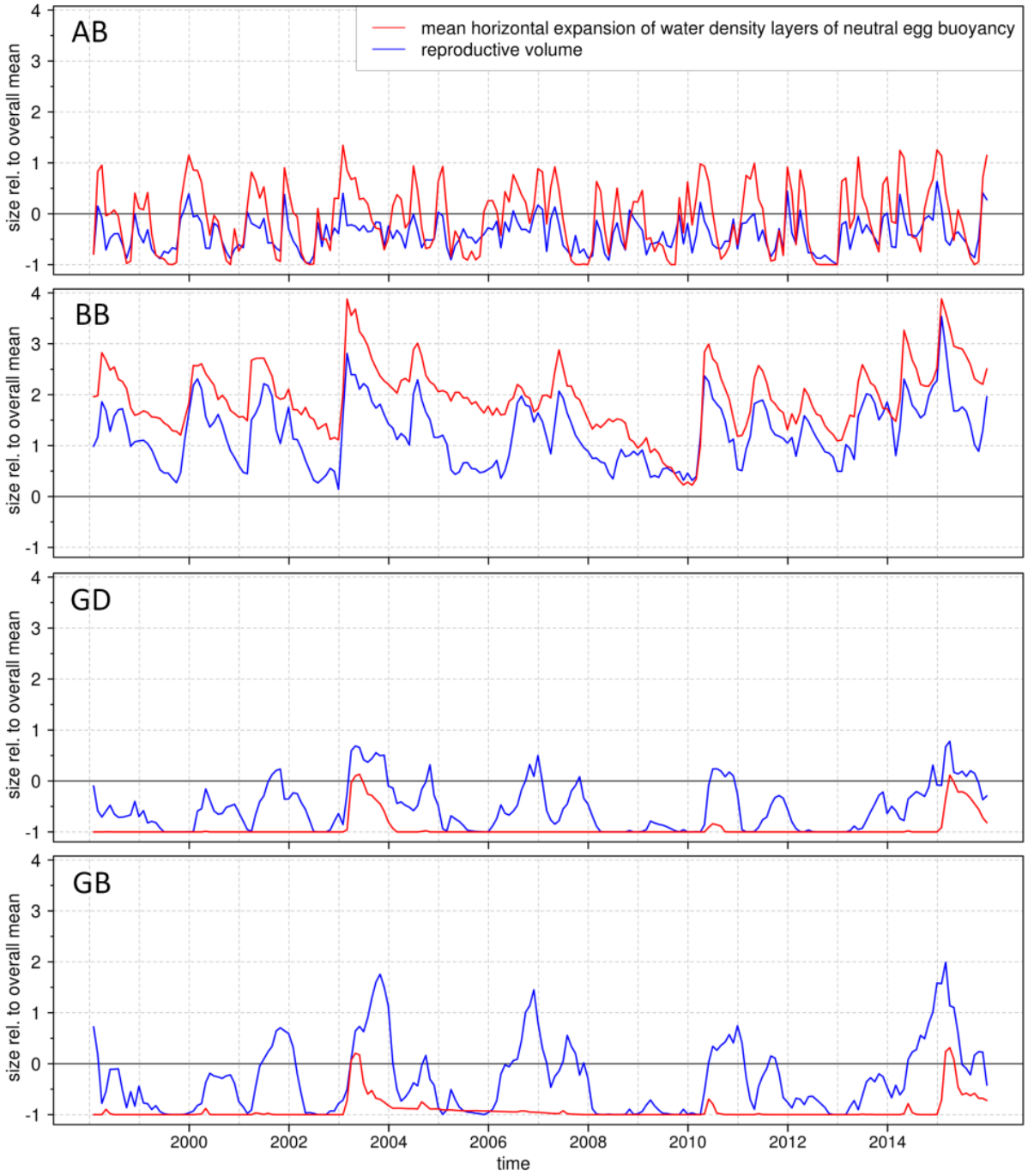

Figure 6: Temporal development of the Reproductive Volume (RV) and the mean horizontal expansion of water density layers of neutral egg buoyancy within the main Baltic Sea sub-basins from 1998 to 2015 (AB: Arkona Basin, BB: Bornholm Basin, GD: Gdansk Deep, GB: Gotland Basin). Shown are relative sizes to an overall mean of each parameter (0 = overall mean, 1 = overall mean x 2 etc.). The horizontal expansion equals the mean expansion of the water density layers corresponding to the neutral egg buoyancies of 7 female spawner size classes

Discussion

Model issues / Eutrophication relevance

The assessments made in this study were based on data for abiotic drivers that were produced by a highly resolved hydrodynamic ocean model. The eutrophication state of the system was modulated by the means of an integrated oxygen sub-model. It simulated

different developments of primary production within the system by modulating oxygen depletion rates. The parameter of the model that realized the changes was adapting on a time scale of years. The model is shown to be in good agreement with in-situ measurements (Lehmann et al., 2014), but is nevertheless a simplification of the highly complex biogeochemical processes within the Baltic Sea, which are influencing the oxygen dynamics on a much smaller time scale. Firstly, the phosphorous and nitrogen cycles are influencing heavily the primary production in the Baltic Sea. They include processes of sedimentation (Hille et al., 2005, 2006; Heiskanen, 1998), ecosystem feedbacks (Vahtera et al., 2007; Kuosa et al., 1997), and nitrification/denitrification (Taylor et al., 2001) also within the bottom sediments (Hall et al., 2017) that are not yet fully understood and predictable (Wulff et al., 1990; Conley et al., 2002; Reissmann et al., 2009). Furthermore, the carbon cycle is as well heavily involved in the determination of the net oxygen content within the Baltic Sea (Schneider et al., 2002; Beldowski et al., 2010; Borges et al., 2010). However, oxygen data produced by the simplified oxygen sub-model, which is not directly including these processes, was used successfully in many publications to asses various aspects of the system related to fisheries science (Voss et al., 2012; Hinrichsen et al., 2011, 2012a, 2012b, 2016). Gustafsson and Omstedt (2009) confirmed with a comparison between modeled and observed data, that the conditions within the deep basins in the Baltic Sea are well represented when assuming constant oxygen consumption rates. The applied oxygen sub-model is following and extending this approach with variable oxygen consumption rates depending on the current temperature and oxygen content (Lehmann et al., 2014). Therefore at present the simplified approach could be seen as beneficial to assess long term characteristics and trends in the system. It is following the dynamic ranges and simulates the mechanistic processes determining the oxygen condition within the Eastern Baltic cod spawning habitat well, but is not divagating into the numerically unsecure details of the system.

Under the HELCOM Baltic Sea action plan (HELCOM, 2007) the level of eutrophication needs to further decrease. However it will take much longer than 2021 until the interannual variability is exceeded by the general reduction trend (Jutterström et al., 2014). From 1995 until now further nutrient inputs (N and P) were decreased by ~20 % (HELCOM, 2017). Other studies combine the projections of increasing precipitation in the region and the associated possible increase of land runoff of allochthonous organic matter to predict an increase in eutrophication (Andersson et al., 2015). The future fate of the Baltic Sea with respect to its eutrophication state is unresolved, which makes studying their impact on the ecosystem challenging (Voss et al., 2011). There is a scientific consensus that the Baltic Sea is still heavily impacted by eutrophication (e.g. HELCOM, 2017). This study is expanding the knowledge on how the spawning habitat of Eastern Baltic cod could react to changes in eutrophication in the system. The relative small response of the cod spawning habitat to a simulated further increase of eutrophication could be an indication that the Baltic Sea is currently close to a state of maximum possible reaction to nutrient forcing.

The parameter quantifying the primary production used in the oxygen sub-model was set to increase by 0.5 within the “pre-experiment” phase from 1970 to 1997. This simulated the doubling of the primary production within the system reported for example in Keiser et al. (1981) for 1970 of 34.85 x 10^6 t C yr^{-1} to 62 x 10^6 t C yr^{-1} as reported in Wasmund et al.

(2001) for 2000. The experimental model runs with a further increase and decrease of the primary production factor until 2015 can therefore be seen as a further increase and decrease to about 80 x 10^6 t C yr^{-1} and 44 x 10^6 t C yr^{-1}, respectively. The future development of the primary production in the Baltic Sea is hard to predict due to the uncertainties of nutrient input development, irregular cyanobacteria blooms (Wasmund et al., 2011) and surface nutrients that are highly sensitive to processes within the sediment (Eilola et al., 2009). The approximation of the total primary production within the Baltic Sea is complex (Gustafsson et al., 2012a; Andersen et al., 2017), which is reflected also in recent publications that expose a lack of understanding of major processes and monitoring data to assess the Baltic Sea primary production state (e.g. Fleming et al., 2015). Therefore the findings of the current study can only be seen as relative indications of the sensitivity of the system to a change in nutrients but not as a comparison between exact eutrophication states. Nevertheless it would be possible to relate the findings to more precise definitions if they would be available in the future.

Reproductive Volume (RV) and Buoyancy Depending Reproductive Layers (BDRL) in comparison

Within the range of tested eutrophication scenarios the approaches to quantify the spawning habitat of Eastern Baltic cod differed substantially. The results for the RV approach suggested that the GD and GB provide regularly suitable spawning habitats of substantial size, whereas the BDRL approach identified only small windows of several months as suitable for eggs spawned by most female size classes. The low availability of spawning habitat in the GD and GB could reduce the reproductive success in these areas to a bare minimum. The BB and AB were identified by the BDRLs as the only sub-basins in the Baltic Sea that provided relevant sizes of spawning habitat within the last 20 years. The BB has here an outstanding role, which was underestimated in previous assessments, which used the RV for habitat mapping. Although Baltic cod was also found to perform spawning migrations (Aro, 1989; Tomkiewicz et al,. 1998; Neuenfeldt et al., 2007; Nielsen et al., 2013) and homing to some degree at least in the western population (Svedäng et al., 2007), it provides one more possible explanation of the current concentration of Eastern Baltic cod to the area around the BB in the south west of the Baltic Proper (Bartolino et al., 2017).

When factoring in the eutrophication state of the system the classical approach missed the impact on the GD environment and underestimated the impact on the most important spawning ground, the BB. The simulated RV data suggested that eutrophication affects either only the BB during stagnation periods or only the GB when the sub-basins are ventilated. Therefore, the RV approach suggests that the eutrophication impact on the spawning habitat of Eastern Baltic cod within all possible future scenarios is significant but restricted locally. To the contrary, the BDRL approach identified a significant impact of eutrophication on all basins. The Impact was most pronounced in the GD and GB but also within the BB an increase of 12 percent points in egg survival chances were found for the scenario of decreasing eutrophication. The BDRL approach provided a higher detailed view on the characteristics of the impact, because it was able to show that the impact is

furthermore depending on spawner size. A significantly larger impact on the egg survival was found for eggs spawned by small females, which had to cope already with smaller habitat sizes and frequently worse oxygen conditions than eggs of larger females. This supports the observation that conditions for eggs spawned by large females of the stock are more influential to stock development, because of the higher survival chances and the less sensitive habitat to environmental change, while eggs spawned by small females can usually not supply a significant amount of recruits (Vallin and Nissling, 2000; Hinrichsen et al., 2016). The eutrophication impact was largest for the smallest size classes and would therefore also have the largest impact on stock development, if the pressure of eutrophication would be reduced.

Recent studies suggest that Eastern Baltic cod is utilizing also the AB more frequently for spawning activities (Hüssy, 2015; Köster et al., 2016). Here no significant impact of eutrophication was found with the RV approach and only a marginal impact could be identified with the BDRL approach. Therefore if Eastern Baltic cod could successfully adapt to the highly eutrophicated state of the Baltic Sea by utilizing predominantly the AB as the main spawning area, it could come to a buffering effect against the lowered reproductive success in the other sub-basins. Köster et al. (2016) also hypothesized, that the recent increase in stock size of Eastern Baltic cod could partly be explained by the increased utilization of the AB as spawning ground. However the conditions for a successful reproduction in the AB are also depending on MBIs, because without these events the salinity conditions here are unable to sustain neutral egg buoyancy (Figure 6 of this study; Köster et al., 2016). The MBIs would also reoxygenate the eastern parts of the Baltic Sea providing suitable spawning habitats there as well (Hinrichsen et al., 2007), which would in turn render the situation in the AB as less important because of the relative small size of the habitat in the AB.

The period of peak spawning activities of Eastern Baltic cod changed in the last decades. Peak spawning was reported to change from April to June in the 70s and 80s (MacKenzie et al., 1996) to the end of July in the 90s (Wieland et al., 2000) and again to a more evenly spread utilization from May to August during the 2000s (Baranova et al., 2011; Köster et al., 2016). These changes had and will have a number of potential consequences for the Eastern Baltic cod stock, for example in terms of temporal overlap with predators and food sources, transport of larvae, egg survival and others (Köster et al., 2016). Therefore we used the RV and BDRL approach to assess the seasonal development of the quality indicators and how the impact of eutrophication would change the habitat suitable for reproduction. The tests with the RV-approach showed a significant difference for the tested time windows (March to May and June to August) only for the GB, but not for other sub-basins. Eutrophication impacted here the seasonal effect significantly. The test results of the BDRL approach showed within all sub-basins but the GB significantly better conditions in terms of spawning habitat quality in the early spawning time window (March to May) compared to later in the season (June to August). The impact of eutrophication was only marginal and similar in both time windows. Therefore both approaches identified eutrophication as a factor that can most likely be neglected next to other factors related to the temporal changes in peak spawning activity, e.g. oxygen (Hinrichsen et al. 2016), ripening of females (Tomkiewicz et al. 2009), or predation (Neumann et al. 2014).

However, RV and BDRL approach differed regionally: while the former placed the confirmed seasonal effect exclusively into the GB, the BDRL approach showed all other sub-basins as affected. Other studies support a seasonal change in the most important BB (e.g. Hinrichsen et al., 2016), that was here missed by the RV approach. Therefore for an assessment of seasonal effects in abiotic factors relevant for cod reproduction, the RV approach proofed to be not sensitive enough, whereas differences could be assessed with the BDRL approach.

Another advantage of the BDRL approach is the possible inclusion of the stressor of acidification for cod egg and larval development (Stiasny et al., 2016). Within the Baltic Sea high oxygen depletion rates in the sub-basins are associated with high levels of ocean acidification and the sub-basins differed strongly in this regard (Figure 3). The range of acidification levels found for the most important spawning ground, the BB, was considerable (~ 0.6 pH units) with the lowest values in eastern sub-basins GD and GB reaching hypercapnia levels of pH<7.4. The physiological processes and mechanisms behind the impact of acidification on Baltic cod are far from fully understood (Stiasny et al., 2016), and there is also considerable inconsistency among experimental results. For Eastern Baltic cod no significant negative effects of experimentally elevated pCO_2 levels to about 4,000 pCO_2 and associated lowered pH to ~7.1 were found on hatching rates, survival and growth within the egg and early larval phase (Frommel et al., 2012a). Also sperm motility of Eastern Baltic cod were found not to be affected by moderate levels of increased CO_2 induced acidification (1360 pCO_2 and pH of approximately 7.55; Frommel et al., 2010). Other studies for Atlantic cod, however, found indications of hypercalcification in otoliths (Maneja et al., 2012b), changes in swimming behavior (Maneja et al., 2012a) and severe tissue damage (Frommel et al., 2012b). Given the large inconsistencies among response variables, prolonged and severe hypercapnia within the spawning habitat is probably not a favorable habitat characteristic, especially when interactions with other stressors are to be considered. Under a possible enhanced eutrophication state of the Baltic Sea further impacts of hypercapnia would be superimposed by hypoxia effects (Reusch et al., 2018). The synergistic effects of hypercapnia and hypoxia are largely unknown and call for further research. The results produced by the BDRL approach, however, would suggest that future experimental studies should include stronger acidification levels as used to date. This would insure that a challenging treatment would be included given the wide range regularly experienced as shown by this study.

The large differences between the results produced by the RV and the BDRL approach are rooted in the mechanistic of the calculations. The RV approach does take a salinity minimum (11 PSU) into account that represents the minimum for cod eggs to achieve neutral buoyancy reported in Grauman (1973). Several recent studies still imply this relationship (e.g. MacKenzie et al., 2000; Plikshs et al., 2015) and responses of the Eastern Baltic cod stock to future modeling scenarios are represented in several studies by the RV (Lindgren et al., 2009; Meier et al., 2012). However, the minimum salinity requirements for neutral egg buoyancy found in studies following these first results were at least 12.3 PSU (Nissling and Westin, 1991; Nissling and Vallin, 1996; 12.5 psu calculated in this study from buoyancies reported in Vallin and Nissling, 2000). Moreover, Hinrichsen et al.

(2016) found a large range in egg buoyancies in the field and Vallin and Nissling (2000) combined all available egg buoyancy data to produce a model showing that the mean buoyancy an egg batch exhibits is correlating with spawner size. Therefore, the RV-concept is applying a minimum salinity level that is enabling potentially only a fraction of all spawned eggs to avoid bottom contact. However, the 11 PSU mark is still representing a relevant factor in cod reproduction: the experimentally found minimum salinity requirements for spermatozoa activation (Westin and Nissling, 1991). But because eggs after fertilization need to be neutral buoyant for a successful development (von Westernhagen, 1970; Wieland, 1995), the current study supports the conclusion that the RV-concept has the weakness to overestimate the reproductive habitat of Eastern Baltic cod.

The refined buoyancy levels offered by the BDRL approach take the age or size structure of the stock into account and could be applied very beneficially in future studies of the spawning habitat. From a stock assessment point of view, as stated also by Eero et al. (2015), good information about the age structure in the stock is of high importance. Large females within the stock contribute immensely to the robustness of the entire population against unfavorable environmental conditions or an anthropogenic reduction of the stock by their potential fecundity (Hixon et al., 2014; Mion et al., 2018; Barneche et al., 2018). We show here that eggs of larger females float above the water layers that become hypoxic during stagnation years and are therefore the size groups within the stock that are also the least impacted by a change in eutrophication. This effect can however be only missed by the RV which is not considering any size depending processes.

Therefore, the BDRL methodology improves our understanding of the dynamics and sensitivity of the spawning habitat of Eastern Baltic cod and demonstrates that the female spawner size should be included in the assessment of reproductive habitat of Eastern Baltic cod in order to not miss important size depending processes. It provides a more detailed and relevant data base for future studies. It could be combined with spatially resolved data of recruitment and/or reproductive processes or success to perform sub-basin depending assessments, leading to a more precise application of abiotic factors within the stock management. The first indication that this could improve the explained variation of stock dynamics was already given by Hinrichsen et al. (2016), where a recruitment model could be significantly improved by the methodology. Therefore, the BDRLs are currently the best approach available to quantify and qualify the spawning habitat of Eastern Baltic cod improving the classical approach of an overall approximation by means of the RV. Future scientific work related to cod stock assessment or environmental impact assessment should consider and possibly further compare and validate the presented BDRL approach.

Conclusions

This study is contributing to the pool of knowledge on the reactions of the system to changes in any direction in the future by testing its sensitivity under different eutrophication scenarios. It shows a clear picture, that the spawning habitat of Eastern Baltic cod is under considerable pressure by hypoxia and hypercapnia, as well as the relative low frequencies of MBIs in the last 2 decades. To lift the pressures and reinforce

the stock the nutrient inputs have to be further reduced and fishing tactics should be reevaluated in regard to fishing pressure and the size structure of the stock to strengthen the ratio of older, larger, repeat spawners within the stock. It further clearly shows the shortfalls of the current practice of environmental considerations in regard to the spawning habitat of Eastern Baltic cod. The proposed BDRL approach gives a more detailed view on the abiotic conditions relevant for reproduction and is able to put precise measures on the egg survival chances of each size class of the stock. On the way forward to a sustainable management of the stock as well as to advances in the scientific knowledge about reproductive processes of Eastern Baltic cod the BDRL approach should be further developed and included.

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Supplementary Material

Table S1: Effect statistics for the impact of female spawner size on oxygen and derived habitat quality parameters on water density layers of neutral egg buoyancy. Response parameters include mean oxygen, oxygen derived pH, oxygen dependent egg survival (y_{surv}) and oxygen dependent larval migration activity (y_{LVMA}). F-values and significance levels are shown sub-basin- and eutrophication scenario specific, indicated in the columns 'basin' and 'Eutrophication scenario' (AB=Arkona Basin, BB=Bornholm Basin, GD=Gdansk Deep, GB=Gotland Basin; Eutrophication scenarios: 30% increase, constant, 30% decrease).

		Response parameter			
		oxygen		pH	
Basin	Eutrophication scenario	F-Value	p value	F-Value	p value
AB	↗	0.51	0.799	0.36	0.907
	→	0.49	0.817	0.34	0.916
	↘	0.47	0.829	0.36	0.906
BB	↗	23.85	<.0001	14.45	<.0001
	→	24.33	<.0001	14.81	<.0001
	↘	24.66	<.0001	14.55	<.0001
GD	↗	1.49	0.206	0.30	0.910
	→	1.27	0.294	0.05	0.994
	↘	1.45	0.220	0.22	0.953
GB	↗	4.21	0.002	3.81	0.003
	→	4.60	0.0007	4.14	0.002
	↘	5.22	0.0002	4.65	0.0007
		y_{surv}		y_{LVMA}	
		F-Value	p value	F-Value	p value
AB	↗	0.58	0.743	0.54	0.775
	→	0.55	0.766	0.28	0.948
	↘	0.55	0.770	0.06	0.999
BB	↗	24.90	<.0001	25.20	<.0001
	→	25.66	<.0001	25.78	<.0001
	↘	26.66	<.0001	26.52	<.0001
GD	↗	1.64	0.163	1.44	0.223
	→	1.34	0.265	1.16	0.338
	↘	1.42	0.229	1.01	0.417
GB	↗	3.15	0.011	5.25	0.0002
	→	4.41	0.001	6.23	<.0001
	↘	6.36	<.0001	7.51	<.0001

Table S2: MANCOVA-type GLM statistical test summary for an overall effect of basin and spawner size/length class on the response parameters of water density layers of neutral egg buoyancy for Eastern Baltic cod derived from the BSIOM oceanographic model run with constant eutrophication. Response parameters were the horizontal expansion and the mean depth of the density layer, as well as the prevailing mean temperature on the density layer.

Main Effect	Statistic	value	F-value	Model DF	Model errors DF	p
Basin	Wilks' Lambda	0.1024	1260.06	9	7311.1	<.0001
	Pillai's Trace	1.3296	797.52	9	9018	<.0001
	Hotelling-Lawley-Spur	4.5512	1518.73	9	4717.4	<.0001
	Roy's Greatest Root	3.2561	3262.58	3	3006	<.0001
Size/length	Wilks' Lambda	0.6730	70.92	18	8497.1	<.0001
	Pillai's Trace	0.3382	63.65	18	9018	<.0001
	Hotelling-Lawley-Spur	0.4690	78.25	18	6003	<.0001
	Roy's Greatest Root	0.4303	215.56	6	3006	<.0001

Table S3: Effect statistics for the impact of early (March to May) or late (June - August) spawning time on habitat quality parameters on water density layers of neutral egg buoyancy. Response parameters include mean oxygen, oxygen derived pH, oxygen dependent egg survival (y_{surv}) and oxygen dependent larval migration activity (y_{LVMA}). Results for the effect fitted to geographical restricted data sets are indicated in the column 'basins included' (AB=Arkona Basin, BB=Bornholm Basin, GD=Gdansk Deep, GB=Gotland Basin, all=All Basins included (overall effect)).

				Type III SS statistics	
Response Variable	Basin included	Effect parameter	Controlled parameter	F-Value	p value
	All	Spawning time	Basin; eutrophication scenario; female size		
Oxygen				635.20	<.0001
pH				706.00	<.0001
y_{surv}				166.54	<.0001
y_{LVMA}				20.79	<.0001
		Spawning time	eutrophication scenario; female size		
Oxygen	AB			4825.39	<.0001
	BB			17.25	<.0001
	GD			24.51	<.0001
	GB			0.36	0.550
pH	AB			4605.39	<.0001
	BB			48.14	<.0001
	GD			6.18	0.014

Table S3 continued				Type III SS statistics	
Response Variable	Basin included	Effect parameter	Controlled parameter	F-Value	p-value
		Spawning time	eutrophication scenario; female size		
pH	GB			2.46	0.118
y_{surv}	AB			2002.03	<.0001
	BB			3.22	0.073
	GD			24.34	<.0001
	GB			0.04	0.843
y_{LVMA}	AB			57.89	<.0001
	BB			3.45	0.063
	GD			29.76	<.0001
	GB			0.00	0.970

Table S4: Seasonal differences in mean oxygen content on water density layers of neutral egg buoyancy. Shown are mean oxygen values of buoyancy levels for each basin and eutrophication scenario separated by early (March to May) or late (June to August) spawning time in the year. Additionally found significant groupings by Scheffé multiple comparison tests following fitted ANCOVA-type GLMs to the data are shown in capital letters, as well as delta oxygen values between the early and late spawning time windows.

		Early spawning (March-May)		Late spawning (June-August)		
Basin	Eutrophication scenario	Scheffé groups	Mean oxygen [ml/l]	Scheffé groups	Mean oxygen [ml/l]	Δ oxygen (early-late) [ml/l]
AB	↗	A	7.69	A	5.63	2.06
	→	B	7.77	B	5.86	1.91
	↘	C	7.86	C	6.11	1.76
BB	↗	A	4.96	A	4.67	0.29
	→	B	5.27	B	4.99	0.28
	↘	C	5.59	C	5.37	0.23
GD	↗	A	4.27	A	3.20	1.07
	→	A	4.67	A	3.66	1.01
	↘	B	5.21	B	4.51	0.70
GB	↗	A	4.89	A	4.02	0.87
	→	A	5.23	A	4.32	0.90
	↘	A	5.51	A	4.81	0.70

Table S5: Mean oxygen content [ml/l] on water density levels of neutral egg buoyancy depending on female spawner size/length class. Results are shown for basin specific tests on the impact of the eutrophication scenario on the oxygen content, including the Arkona Basin (AB), Bornholm Basin (BB), Gdansk Deep (GD) and Gotland Basin (GB) (Figure 1). The fitted GLM included time as covariate and eutrophication scenario as main effect. The GD and GB size/length classes < 61cm were excluded due to insufficient amount of data points. Additionally the delta oxygen value between the eutrophication scenarios is shown for each group.

		Mean oxygen [ml/l] in Eutrophication scenario				
Basin	Size/length class [cm]	↗	↘	Δ oxygen [ml/l]	F-value	p-value
AB	21-37	6.71	7.03	0.31	1.41	0.247
	38-49	6.71	7.05	0.34	1.82	0.165
	50-60	6.70	7.03	0.33	1.78	0.171
	61-69	6.78	7.09	0.31	1.74	0.177
	70-76	6.85	7.15	0.30	1.75	0.175
	77-83	6.84	7.14	0.30	1.87	0.156
	>84	6.49	7.22	0.28	1.79	0.169
BB	21-37	3.82	4.50	0.68	3.25	0.04
	38-49	4.11	4.86	0.75	5.02	0.007
	50-60	4.48	5.20	0.72	5.61	0.004
	61-69	4.86	5.54	0.68	6.62	0.002
	70-76	5.20	5.84	0.64	7.61	0.0006
	77-83	5.40	6.01	0.61	8.35	0.0003
	>84	5.85	6.39	0.54	10.33	<.0001
GD	61-69	3.40	4.58	1.19	7.65	0.002
	70-76	3.48	4.66	1.18	9.88	0.0005
	77-83	3.92	5.03	1.11	3.82	0.031
	>84	4.30	5.24	0.95	4.55	0.014
GB	70-76	4.55	5.46	0.92	2.37	0.104
	77-83	4.65	5.46	0.81	2.70	0.074
	>84	3.17	3.73	0.56	0.77	0.466

Table S6: Coefficients and statistics of the decadal dependency of the prevailing pH from the oxygen content within in situ measurements of the last 40 years taken from the ICES Oceanographic data base. Shown are regression results for horizontally and vertically selected bodies of water. Horizontally sub-basins were selected after adapted ICES sub-divisions (Fig 1, AB= Arkona Basin, BB= Bornholm Basin, GD= Gdansk Deep and GB = Gotland Basin). Vertical separations were orientated on the usual depth of the permanent halocline.

Basin	depth limits [m]	decade	y_0	slope	R^2	adj. R^2	st. error	F	Df. Resid	p
AB	24–45	1990	7.417	0.085	0.672	0.670	0.118	554.1	271	<0.0001
		2000	7.452	0.080	0.551	0.546	0.120	110.4	90	<0.0001
	45–60	1990	7.571	0.070	0.495	0.456	0.146	12.7	13	0.003
		2000	7.527	0.069	0.780	0.767	0.076	56.8	16	<0.0001
BB	41–77	1990	7.278	0.097	0.669	0.668	0.159	1067.2	528	<0.0001
		2000	7.245	0.090	0.817	0.817	0.096	2382.6	534	<0.0001
	77–110	1990	7.369	0.088	0.310	0.307	0.200	119.3	266	<0.0001
		2000	7.332	0.058	0.362	0.359	0.095	132.5	234	<0.0001
GD	60–96	1990	7.351	0.091	0.550	0.548	0.201	503.7	413	<0.0001
		2000	7.221	0.088	0.698	0.698	0.169	1259.7	544	<0.0001
	96–120	1990	7.408	0.086	0.297	0.292	0.228	55.9	132	<0.0001
		2000	7.283	0.077	0.343	0.333	0.112	34.4	66	<0.0001
GB	55–123	1990	7.156	0.105	0.787	0.787	0.150	6270.8	1699	<0.0001
		2000	7.203	0.092	0.817	0.817	0.127	6507.2	1454	<0.0001
	123–260	1990	7.264	0.024	0.045	0.044	0.102	36.5	778	<0.0001
		2000	7.252	0.065	0.267	0.266	0.067	315.4	868	<0.0001

References (Chapter 3)

Andersen, J. H., J. Carstensen, D. J. Conley, K. Dromph, V. Fleming-Lehtinen, B. G. Gustafsson, A.B. Josefson, A. Norkko, et al., 2017. Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. Biol Rev, 92: 135–149.

Andersson, A., H.E.M. Meier, M. Ripszam, O. Rowe, J. Wikner, P. Haglund, … R. Elmgren, 2015. Projected future climate change and Baltic Sea ecosystem management. Ambio, 44(Suppl 3), 345–356. doi: 10.1007/s13280-015-0654-8.

Aro, E., 1989. A review of fish migration patterns in the Baltic. Rapp. P.-v. Réun. Cons. Int. Explor. Mer. 190:72–96.

Baranova, T., B. Müller-Karulis, I. Sics, and M. Plikshs, 2011. Changes in the annual life cycle of Eastern Baltic Cod during 1950-2010. ICES Document CM 2011/R: 10.

Barneche, D. R., D. R. Robertson, C. R. White and D. J. Marshall, 2018. Fish reproductive-energy output increases disproportionately with body size. Science 360 (6389), 642-645. DOI: 10.1126/science.aao6868

Bartolino, V., H. Tian, U. Bergstrøm, P. Jounela, E. Aro, C. Dieterich, et al., 2017. Spatio-temporal dynamics of a fish predator: Density-dependent and hydrographic effects on Baltic Sea cod population. PLoS ONE 12(2): e0172004. doi:10.1371/journal.pone.0172004.

Beldowski, J., A. Löffler, B. Schneider, L. Joensuu, 2010. Distribution and biogeochemical control of total CO2 and total alkalinity in the Baltic Sea. Journal of Marine Systems 81:252-259.

Borges, A. V., and N. Gypens, 2010. Carbonate chemistry in the coastal zone responds more strongly to eutrophication than to ocean acidification. Limnology and Oceanography 55:346-353.

Bumke, K., U. Karger, L. Hasse, and K. Niekamp, 1998. Evaporation over the Baltic Sea as an example of a semi-enclosed sea. Contributions to Atmospheric Physics 71:249-261.

Carstensen, J., J. H. Andersen, B. G. Gustafsson, and D. J. Conley, 2014. Deoxygenation of the Baltic Sea during the last century. Proceedings of the National Academy of Sciences of the United States of America 111:5628-5633.

Conley, D.J., C. Humborg, L. Rahm, O.P. Savchuk, F. Wulff, 2002. Hypoxia in the Baltic Sea and Basin-Scale Changes in Phosphorus Biogeochemistry. Environmental Science & Technology 2002 36 (24), 5315-5320. DOI: 10.1021/es025763w.

Dee, D. P., S. M. Uppala, A. J. Simmons, P. Berrisford, P. Poli, S. Kobayashi, U. Andrae et al., 2011. The ERA-Interim reanalysis: configuration and performance of the data assimilation system. Quarterly Journal of the Royal Meteorological Society 137:553-597.

Eero, M., J. Hjelm, J. Behrens, K. Buchmann, M. Cardinale, M. Casini, P. Gasyukov et al., 2015. Eastern Baltic cod in distress: biological changes and challenges for stock assessment. ICES Journal of Marine Science 72:2180-2186.

Eilola, K., M. Meier, and E. Almroth-Rosell, 2009. On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study, v. 75.

Elken, J. and W. Matthäus, 2008. Physical system description. The BACC Author Team (von Storch, H.). Assessment of Climate Change for the Baltic Sea Basin. Series: Regional climate studies. Springer-Verlag, Berlin, Heidelberg, pp. 379–398.

Fleming, V., J. Andersen, J. Carstensen, E. Łysiak-Pastuszak, C. Murray, M. Pyhälä, M. Laamanen, 2015. Recent developments in assessment methodology reveal that the Baltic Sea eutrophication problem is expanding. Ecological Indicators. 48. 380–388. 10.1016/j.ecolind.2014.08.022.

Frommel, A., A. Schubert, U. Piatkowski, and C. Clemmesen, 2012a. Egg and early larval stages of Baltic cod, Gadus morhua , are robust to high levels of ocean acidification. Marine Biology:1-10.

Frommel, A. Y., R. Maneja, D. Lowe, A. M. Malzahn, A. J. Geffen, A. Folkvord, U. Piatkowski et al., 2012b. Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. Nature Climate Change 2:42-46.

Frommel, A. Y., V. Stiebens, C. Clemmesen, and J. Havenhand. 2010. Effect of ocean acidification on marine fish sperm (Baltic cod: Gadus morhua). Biogeosciences 7:3915-3919.

GFortran, Gnu compiler collection (gcc) version 4.6.3, Copyright © 2011 Free Software Foundation, Inc. http://gcc.gnu.org/.

Grauman, G. B., 1973. Investigations of factors influencing fluctuations in abundance of Baltic cod. Rapp. P.-v. Reun. Cons, int Explor. Mer, 164: 73-76.

Grønkjær, P., K. Wieland, 1997. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Marine Ecology Progress Series 154, 91–105.

Grønkjær, P., C. Clemmesen, and M.A. St. John, 1997. Nutritional condition and vertical distribution of Baltic cod larvae. Journal of Fish Biology 51, 352–369.

Gustafsson, E.O. and A. Omstedt, 2009. Sensitivity of Baltic Sea deep water salinity and oxygen concentration to variations in physical forcing. Boreal Env. Res. 14: 18-30.

Gustafsson, B. G., F. Schenk, T. Blenckner, K. Eilola, H. E. M. Meier, B. Muller-Karulis, T. Neumann et al., 2012a. Reconstructing the Development of Baltic Sea Eutrophication 1850-2006. Ambio 41:534-548.

Gustafsson, E., 2012b. Modelled long-term development of hypoxic area and nutrient pools in the Baltic Proper. Journal of Marine Systems 94:120-134.

Hall, P.O.J., E. Almroth Rosell, S. Bonaglia, A.W. Dale, A. Hylén, M. Kononets, M.Nilsson, et al., 2017. Influence of Natural Oxygenation of Baltic Proper Deep Water on Benthic Recycling and Removal of Phosphorus, Nitrogen, Silicon and Carbon. Front. Mar. Sci. 4:27. doi: 10.3389/fmars.2017.00027.

Heiskanen, A.-S., 1998. Factors governing sedimentation and pelagic nutrient cycles in the northern Baltic Sea. Monogr. Bor. Env. Res. 1998, 8, 1– 80.

HELCOM, 2007. Climate Change in the Baltic Sea Area – HELCOM Thematic Assessment in 2007. Baltic Sea Environment Proceedings No. 111.

HELCOM, 2013 Climate change in the Baltic Sea Area: HELCOM thematic assessment in 2013. Balt. Sea Environ. Proc. No. 137.

HELCOM, 2017. Baltic Sea Environment Proceedings No. 150. ISSN: 0357-2994.

Hille, S., T. Leipe, T. Seifert, 2006. Spatial variability of recent sedimentation rates in the Eastern Gotland Basin (Baltic Sea). Oceanologia. 48.

Hille, S., G. Nausch, T.Leipe, 2005. Sedimentary deposition and reflux of phosphorus (P) in the Eastern Gotland Basin and their coupling with the water column P concentrations. Oceanologia 47 (4), 1–17.

Hinrichsen, H. H., K. Hussy, and B. Huwer. 2012a. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics. Ices Journal of Marine Science 69:1744-1752.

Hinrichsen, H. H., B. Huwer, A. Makarchouk, C. Petereit, M. Schaber, and R. Voss. 2011. Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (Gadus morhua). Ices Journal of Marine Science 68:2019-2028.

Hinrichsen, H. H., W. Kuhn, M. A. Peck, and R. Voss. 2012b. The impact of physical and biological factors on the drift and spatial distribution of larval sprat: A comparison of the Baltic and North Seas. Progress in Oceanography 107:47-60.

Hinrichsen, H. H., B. von Dewitz, J. Dierking, H. Haslob, A. Makarchouk, C. Petereit, and R. Voss. 2016. Oxygen depletion in coastal seas and the effective spawning stock biomass of an exploited fish species. Royal Society Open Science 3.

Hinrichsen, H. H., R. Voss, K. Wieland, F. Koster, K. H. Andersen, and P. Margonski. 2007. Spatial and temporal heterogeneity of the cod spawning environment in the Bornholm Basin, Baltic Sea. Marine Ecology-Progress Series 345:245-254.

Hixon, M.A., D.W. Johnson and S.M. Sogard, 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science 71, 2171–2185. doi: 10.1093/icesjms/fst200.

Huwer, B., C. Clemmesen, P. Gronkjaer, and F. W. Köster, 2011. Vertical distribution and growth performance of Baltic cod larvae - Field evidence for starvation-induced recruitment regulation during the larval stage? Progress in Oceanography 91:382-396.

Hüssy, K., H.-H. Hinrichsen, M. Eero, H. Mosegaard, J. Hemmer-Hansen, A. Lehmann, and L.S. Lundgaard, 2015. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment. – ICES Journal of Marine Science, doi: 10.1093/icesjms/fsv227.

ICES Dataset on Ocean Hydrography. 2009. The International Council for the Exploration of the Sea, Copenhagen.

Jutterström, S., H. C. Andersson, A. Omstedt, and J. M. Malmaeus, 2014. Multiple stressors threatening the future of the Baltic Sea–Kattegat marine ecosystem: Implications for policy and management actions. Marine Pollution Bulletin 86:468-480.

Kaiser, W., H. Renk, and S. Schulz, 1981. Die Primärproduktion der Ostsee. Geodätische und Geophysikalische Veröffentlichungen, Reihe IV 33, 27–52.

Keller, K., R. D. Slater, M. Bender, and R. M. Key, 2001. Possible biological or physical explanations for decadal scale trends in North Pacific nutrient concentrations and oxygen utilization. Deep Sea Research Part II: Topical Studies in Oceanography 49:345-362.

Kelley, D., 2011. oce: Analysis of Oceanographic data. R package version 0.5-1. http://CRAN.R-project.org/package=oce.

Köster, F. W., C. Mollmann, H.-H. Hinrichsen, K. Wieland, J. Tomkiewicz, G. Kraus, R. Voss et al., 2005. Baltic cod recruitment - the impact of climate variability on key processes. Ices Journal of Marine Science 62:1408-1425.

Köster, F. W., B. Huwer, H.-H. Hinrichsen, V. Neumann, A. Makarchouk, M. Eero, B. von Dewitz, K. Hüssy, et al., 2016. Eastern Baltic cod recruitment revisited—dynamics and impacting factors. ICES Journal of Marine Science, doi:10.1093/icesjms/fsw172.

Kronsell, J. and P. Andersson, 2012. Total Regional Runoff to the Baltic Sea. HELCOM Indicator Fact Sheets 2011. Online http://www.helcom.fi/environment2/ifs.

Kuosa, H., R. Autio, P. Kuuppo, O. Setälä, S. Tanskanen, 1997. Nitrogen, silicon and zooplankton controlling the Baltic spring bloom: an experimental study. Estuar. Coast. Shelf Sci. 1997, 45, 813– 821.

Lehmann, A., 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. Tellus A 47:1013-1031.

Lehmann, A., and H.-H. Hinrichsen, 2000. On the thermohaline variability of the Baltic Sea. Journal of Marine Systems 25:333-357.

Lehmann, A., W. Krauss, and H.-H. Hinrichsen, 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus Series a-Dynamic Meteorology and Oceanography 54:299-316.

Lehmann, A., K. Getzlaff, and J. Harlass, 2011. Detailed assessment of climate variability in the Baltic Sea area for the period 1958 to 2009. Climate Research 46:185-196.

Lehmann, A., H.-H. Hinrichsen, K. Getzlaff, K. Myrberg, 2014. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. J. Mar. Syst. 134, 20–28. doi:10.1016/j.jmarsys.2014.02.012.

Lindegren, M., C. Möllmann, A. Nielsen, N.C. Stenseth, 2009. Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. Proceedings of the National Academy of Sciences Aug 2009, 106 (34) 14722-14727; doi:10.1073/pnas.0906620106.

MacKenzie, B. R., M.A. St. John, and K. Wieland, 1996. Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. Marine Ecology Progress Series 134: 265–281.

MacKenzie, B. R., H.-H. Hinrichsen, M. Plikshs, K. Wieland, and A.S. Zezera, 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod Gadus morhua eggs in the Baltic Sea. Marine Ecology-Progress Series 193:143-156.

Maneja, R.H., A.Y. Frommel, H.I. Browman, C. Clemmesen, A.J. Geffen, A. Folkvord, U. Piatkowski, et al., 2012a. The swimming kinematics of larval Atlantic cod, Gadus morhua L., are resilient to elevated seawater pCO 2. Marine Biology:1-10.

Maneja, R. H., A.Y. Frommel, A.J. Geffen, A. Folkvord, U. Piatkowski, M.Y. Chang, and C. Clemmesen, 2012b. Effects of ocean acidification on the calcification of otoliths

of larval Atlantic cod, Gadus morhua L. EGU General Assembly Conference Abstracts 14:1070.

Margonski, P., S. Hansson, M. T. Tomczak, and R. Grzebielec, 2010. Climate influence on Baltic cod, sprat, and herring stock-recruitment relationships. Progress in Oceanography 87:277-288.

Meier, M., H.C. Andersson, K. Eilola, B.G. Gustafsson, I. Kuznetsov, B. Muller-Karulis, T. Neumann, O. Savchuk, 2011. Hypoxia in future climates: A model ensemble study for the Baltic Sea. Geophysical Research Letters. 38. 6. 10.1029/2011GL049929.

Meier HE, B. Müller-Karulis, H.C. Andersson, C. Dieterich, K. Eilola, B.G. Gustafsson, A. Höglund, R. Hordoir, et al., 2012a. Impact of climate change on ecological quality indicators and biogeochemical fluxes in the Baltic sea: a multi-model ensemble study. Ambio. 2012 Sep; 41(6):558-73.

Melzner, F., J. Thomsen, W. Koeve, A. Oschlies, M. Gutowska, H. Bange, H. Hansen et al., 2012. Future ocean acidification will be amplified by hypoxia in coastal habitats. Marine Biology:1-14.

Millero, F. J., and K. Kremling. 1976. Densities of Baltic Sea waters. Deep-Sea Research 23:1129-1138.

Mion, M., A. Thorsen, F. Vitale, J. Dierking, J.P. Herrmann, B. Huwer, B. von Dewitz and M. Casini, 2018. Effect of fish length and nutritional condition on the fecundity of distressed Atlantic cod Gadus morhua from the Baltic Sea. J Fish Biol. doi:10.1111/jfb.13563.

Neuenfeldt, S., H.-H. Hinrichsen, A. Nielsen, and K.H. Andersen, 2007. Reconstructing migrations of individual cod (Gadus morhua L.) in the Baltic Sea by using electronic data storage tags. Fisheries Oceanography 16:526-535.

Neumann, V., F.W. Köster, M. Schaber, and M. Eero, 2014. Recovery in eastern Baltic cod: is increased recruitment caused by decreased predation on early life stages? ICES Journal of Marine Science 71: 1382–1392.

Nielsen JR, B. Lundgren, K. Kristensen, F. Bastardie, 2013. Localisation of Nursery Areas Based on Comparative Analyses of the Horizontal and Vertical Distribution Patterns of Juvenile Baltic Cod (Gadus morhua). PLoS ONE 8(8): e70668. https://doi.org/10.1371/journal.pone.0070668.

Nissling, A., and L. Westin, 1991. Egg buoyancy of Baltic cod (Gadus morhua) and its implications for cod stock fluctuations in the Baltic. Marine Biology 111:33-35.

Nissling, A., and L. Vallin, 1996. The ability of Baltic cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. Journal of Fish Biology 48:217-227.

Oschlies, A., K.G. Schultz, U. Riebesell, A. Schmittner, 2008. Simulated 21 century's increase in oceanic suboxia in CO2-enhanced biotic carbon export. Global Biogeochem. Cycles 22, GB4008, doi 10.1029/2007GB003147.

Pliksh, M., M. Kalejs, G. Graumann, 1993. The influence of environmental conditions and spawning stock size on the year class strength of the eastern Baltic cod. ICES CM 1993/J:22.

Plikshs, M., H.-H. Hinrichsen, D. Elferts, I. Sics, G. Kornilovs, and F. W. Köster, 2015. Reproduction of Baltic cod, Gadus Morhua (Actinopterygii: Gadiformes: Gadidae), in the Gotland Basin: Causes of Annual Variability. Acta Ichthyologica Et Piscatoria 45:247-258.

Reissmann, J.H., H. Burchard, R. Feistel, E. Hagen, H.U. Lass, V. Mohrholz, G. Nausch, L. Umlauf, and G. Wieczorek, 2009. Vertical mixing in the Baltic Sea and consequences for eutrophication — a review. Prog. Oceanogr. 82, 47–80. doi 10.1016/j.pocean.2007.10.004.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., et al., 2018. The Baltic Sea as a time machine for the future coastal ocean. [10.1126/sciadv.aar8195]. Science Advances, 4(5).

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rudolph, C., and A. Lehmann, 2006. A model-measurements comparison of atmospheric forcing and surface fluxes of the Baltic Sea. Oceanologia 48 (3), 333–380.

Rohlf, N. 1999. Aktivität und Vertikalwanderung der Larven des Ostseedorsches (Gadus morhua callarias) während der Dottersackphase. PhD thesis, Institute of Marine Sciences, Kiel. Berichte Institut für Meereskunde Kiel, Nr. 312. 60 pp.

Scheffé, H., 1959. The Analysis of Variance, New York: John Wiley & Sons.

Schneider, B., G. Nausch, H. Kubsch, and I. Petersohn, 2002. Accumulation of total CO2 in the Baltic Sea deep water and its relationship to nutrient and oxygen concentrations. Mar. Chem. 77, 277–291.

Soetaert, K., T. Petzholdt, and F. Meysman, 2012. marelac: Tools for Aquatic Sciences. R package version 2.1.2. http://CRAN.R-project.org/package=marelac.

Stiasny, M.H., F.H. Mittermayer, M. Sswat, R. Voss, F. Jutfelt, M. Chierici, et al., 2016. Ocean Acidification Effects on Atlantic Cod Larval Survival and Recruitment to the Fished Population. PLoS ONE 11(8): e0155448. doi:10.1371/journal.pone.0155448.

Stramma, L., S. Schmidtko, L. A. Levin, and G. C. Johnson, 2010. Ocean oxygen minima expansions and their biological impacts. Deep-Sea Research Part I-Oceanographic Research Papers 57:587-595.

Svedäng, H., D. Righton, and P. Jonsson, 2007. Migratory behavior of Atlantic cod Gadus morhua: natal homing is the prime stock separating mechanism. Marine Ecology Progress Series, 345: 1–12.

Taylor, G. T., M. Iabichella, T.-Y. Ho, M.I. Scranton, R.C. Thunell, F. Muller-Karger, and R. Varela, 2001. Chemoautotrophy in the redox transition zone of the Cariaco Basin: A significant mid-water source of organic carbon production. Limnol. Oceanogr. 2001, 46, 148– 163.

Tomkiewicz, J., K.M. Lehmann, and M.A. St John, 1998. Oceanographic influences on the distribution of Baltic cod, Gadus morhua, during spawning in the Bornholm Basin of the Baltic Sea. Fish Oceanogr 7: 48−62.

Tomkiewicz, J., J.G. Støttrup, C. Jacobsen, M.C. Røjbek, and F.W. Köster, 2009. Influence of lipids and fatty acid composition in Eastern Baltic cod (Gadus morhua L.) and its

prey with emphasis on the timing of maturation and spawning. ICES C.M. 2009/C: 10.

Tukey, J. W., 1953. The Problem of Multiple Comparisons. In H. I. Braun, ed., The Collected Works of John W. Tukey, volume 8, 1994, New York: Chapman and Hall.

Vahtera, E., D.J. Conley, B.G. Gustafsson, H. Kuosa, H. Pitkänen, O.P. Savchuk, T. Tamminen, M. Viitasalo, et al., 2007. Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. Ambio 2007, 36, 186– 194.

Voss, M., J.W. Dippner, C. Humborg, J. Hürdler, F. Korth, T. Neumann, G. Schernewski, and M. Venohr, 2011. History and scenarios of future development of Baltic Sea eutrophication. Estuarine, Coastal and Shelf Science, 92, 3: 307-322, ISSN 0272-7714, doi: 10.1016/j.ecss.2010.12.037.

Vallin, L., A. Nissling, 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, Gadusmorhua: Implications for stock structure effects on recruitment. Fisheries Research. 21-37.

Voss, R., C. Petereit, J.O. Schmidt, A. Lehmann, A. Makarchouk, and H.-H. Hinrichsen, 2012. The spatial dimension of climate-driven temperature change in the Baltic Sea and its implication for cod and sprat early life stage survival. Journal of Marine Systems 100:1-8.

Wasmund, N., A. Andrushaitis, E. Łysiak-Pastuszak, B. Müller-Karulis, G. Nausch, T. Neumann, H. Ojaveer, I. Olenina, et al., 2001. Trophic status of the south-eastern Baltic Sea: a comparison of coastal and open areas. Estuar. Coast. Shelf Sci. 53, 849–864.

Wasmund, N., J. Tuimala, S. Suikkanen, L. Vandepitte, and A. Kraberg, 2011. Long-term trends in phytoplankton composition in the western and central Baltic Sea. Journal of Marine Systems 87:145-159.

von Westernhagen, H., 1970. Erbrüten der Eier von Dorsch (Gadus morhua), Flunder (Pleuronectes flesus) and Scholle (Pleuronectes platessa) unter kombinierten Temperatur- und Salzgehaltsbedingungen. Helgoländer Wissenschaftliche Meeresuntersuchungen, 21: 21–102.

Westin, L., and A. Nissling, 1991. Effects of salinity on spermatozoa motility, percentage of fertilized eggs and egg development of Baltic cod (Gadus morhua), and implications for cod stock fluctuations in the Baltic. Marine Biology 108:5-9.

Wieland K., U. Waller, and D. Schnack, 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10: 163‑177.

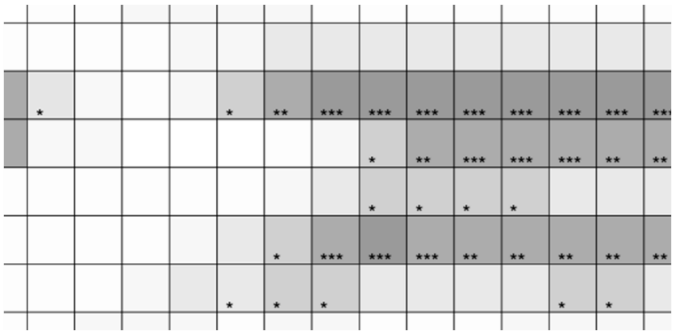
Wieland, K. 1995. Einfluss der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (Gadus morhua callanas) im Bornholmbecken, südliche zentrale Ostsee. Berichte aus dem Institut fur Meereskunde an der Christian-Albrechts-Universitat zu Kiel, no. 266.

Wieland, K., A. Jarre-Teichmann, and K. Horbowa, 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science 57: 452–464.

Wulff, F., A. Stigebrandt, and L. Rahm, 1990. Nutrient Dynamics of the Baltic Sea. Ambio, 19(3), 126-133. Retrieved from http://www.jstor.org/stable/4313678.

Zillén, L., J.D. Conley, T. Andrén, E. Andrén, and S. Björck, 2008. Past occurrences of hypoxia in the Baltic Sea and the role of climate variability, environmental change and human impact. Earth-Science Reviews 91, Issues 1–4, 77-92, doi 10.1016/j.earscirev.2008.10.001.

Chapter 4



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Use of existing hydrographic infrastructure to forecast the environmental spawning conditions for Eastern Baltic Cod

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Abstract

The semi-enclosed nature and estuarine characteristics, together with its strongly alternating bathymetry, make the Baltic Sea prone to much stronger interannual variations in the abiotic environment, than other spawning habitats of Atlantic cod (*Gadus morhua*). Processes determining salinity and oxygen conditions in the basins are influenced both by long term gradual climate change, e.g. global warming, but also by short-term meteorological variations and events. Specifically one main factor influencing cod spawning conditions, the advection of highly saline and well-oxygenated water masses from the North Sea, is observed in irregular frequencies and causes strong interannual variations in stock productivity. This study investigates the possibility to use the available hydrographic process knowledge to predict the annual spawning conditions for Eastern Baltic cod in its most important spawning ground, the Bornholm Basin, only by salinity measurements from a specific location in the western Baltic. Such a prediction could serve as an environmental early warning indicator to inform stock assessment and management. Here we used a hydrodynamic model to hindcast hydrographic property fields for the last 40+ years. High and significant correlations were found for months early in the year between the 33m salinity level in the Arkona Basin and the oxygen-dependent cod

spawning environment in the Bornholm Basin. Direct prediction of the Eastern Baltic cod egg survival in the Bornholm Basin based on salinity values in the Arkona Basin at the 33 m depth level is shown to be possible for eggs spawned by mid-age and young females, which currently predominate the stock structure. We recommend to routinely perform short-term predictions of the Eastern Baltic cod spawning environment, in order to generate environmental information highly relevant for stock dynamics. Our statistical approach offers the opportunity to make best use of permanently existing infrastructure in the western Baltic to timely provide scientific knowledge on the spawning conditions of Eastern Baltic cod. Furthermore it could be a tool to assist ecosystem-based fisheries management with a cost-effective implementation by including the short term predictions as a simple indicator in the annual assessments.

Introduction

Climate and anthropogenic forcing induce a highly variable abiotic environment in the Baltic Sea [1]. All major Baltic fish populations are affected by the environmental variability both with respect to growth and recruitment. For example, the growth rates of herring and sprat diminish with reduced salinity in the eastern and northern part of the Baltic [2,3]. It has also been indicated that the recruitment of sprat in the entire Baltic is significantly correlated to temperature [4] as well as to wind-driven larval transport patterns [5]. Abiotic variations translate over physiological processes and food web dynamics into changes in fish stock productivity [6], and hence challenge sustainable fisheries management [7]. However, recruitment estimates in the assessment procedure currently employed do not include any environmental factors, and hence neglect these processes [8]. In the Baltic the fishing industry as well as consumer representatives have expressed a major interest in relative year-to-year stability of catch options, determining the total amount of permitted catch per species [9,10]. Inclusion of environmental factors in the assessments with short-term forecasts of environmental conditions, possibly enhancing the recruitment estimations for the coming year might be a way forward towards more environmental orientated and stable advice on sustainable catches.

Here, we concentrate on Eastern Baltic cod, which is of high ecological as well as economic importance and is historically the third largest Atlantic cod stock[11]. The stock is distributed in the south-eastern Baltic Sea with the main spawning grounds being the Bornholm Basin, the Gdansk Deep and the Gotland Basin, and additionally it is sharing the Arkona Basin with the western Baltic cod stock [12] (Fig 1). Since the onset of sufficiently detailed records around 1966, the stock showed large fluctuations in stock size, growth, and especially recruitment [13] which have been shown to strongly depend on various environmental factors [13-15]. During the end of the 1980s the stock drastically declined [16] due to a combination of overfishing and the absence of major Baltic inflow events [17], resulting in bad environmental conditions, both in terms of sufficient salinity and oxygen conditions for reproduction in the sub-basins. Currently, the stock seems to be in a regime of comparatively low productivity with indications of an upward trend [15].

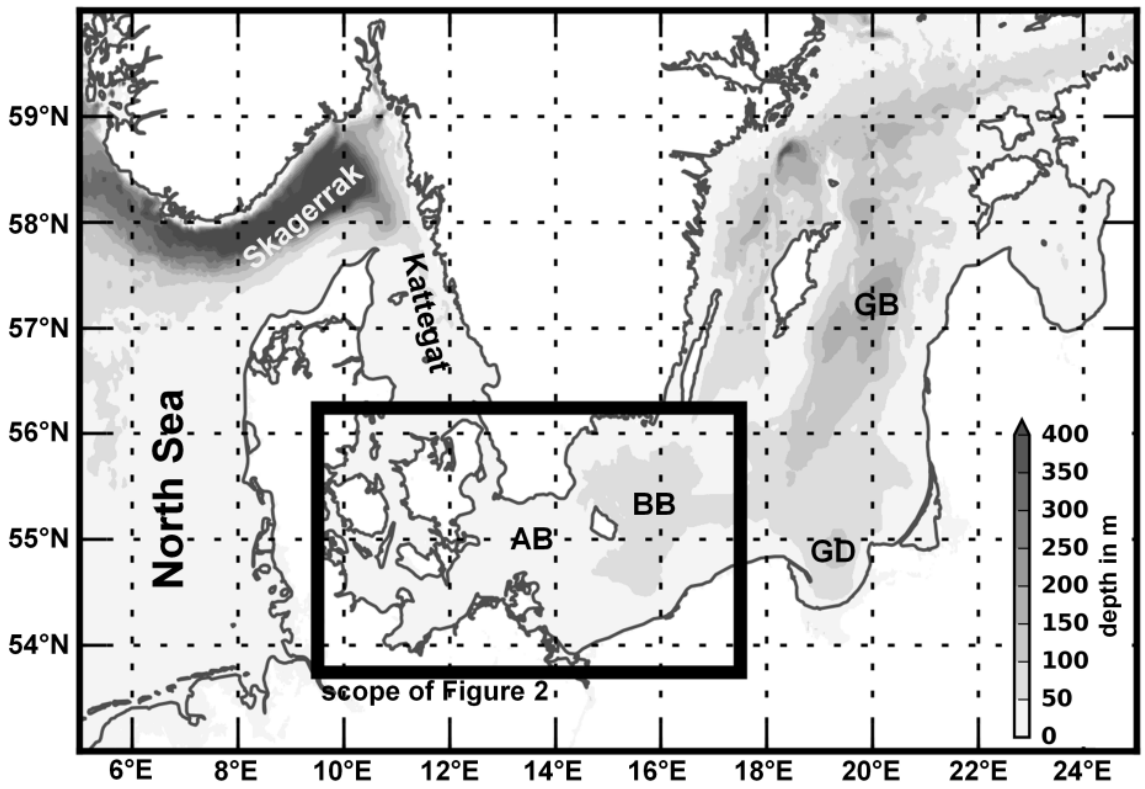

Figure 1: Overview of the Baltic Sea region. Main basins of the Baltic Sea are indicated in abbreviated form by AB (Arkona Basin), BB (Bornholm Basin), GD (Gdansk Deep) and GB (Gotland Basin). The black frame indicates the scope of the more detailed map in Fig 2. Bathymetric data ETOPO1 are taken from Amante and Eakins [18].

Recruitment is both related to egg production but also to egg survival probability depending on hydrographic conditions and predation [14,15]. Based on experimentally established thresholds of salinity, temperature and oxygen for egg survival, MacKenzie et al. [19] quantified the volume of water that permitted successful Eastern Baltic cod egg development, the reproductive volume. Spatial comparisons demonstrated extensive differences between the three main spawning areas, i.e. the Bornholm Basin, Gdansk Deep, and Gotland Basin (Fig 1). The reproductive volume was highly variable in the last 60 years but was found on generally low levels since 1980 [19]. In recent years, only the Bornholm Basin remained as a major spawning ground, due to regular occurrence of hypoxic conditions at the other two historic spawning sites [20].

The main factor determining the dynamics of suitable water masses for cod reproduction in the Eastern Baltic Sea is the advection of highly saline and well-oxygenated water masses from the North Sea and Kattegat area (Fig 1). These water masses enter the central Baltic Sea through the Great Belt and the Øresund (Fig 2). Schinke and Matthäus [21] identified the occurrence of high atmospheric pressure associated with easterly winds followed by longer time periods of westerly gales over the North Atlantic and Europe, with only small fluctuations in direction, as principle major Baltic inflow mechanisms. Stigebrandt [22] showed that the inflowing water before entering the Bornholm Basin forms a pool in the deeper part of the Arkona Basin. In general, the inflowing saline water masses manifest as density-driven bottom gravity currents that entrain ambient surface water and interleave at levels of neutral buoyancy along the cascade of sub-basins [23]. But hydrodynamic

modelling exercises performed by Krauß and Brügge [24] showed that further processes such as wind-induced return flows are important for the exchange of deep water masses between the sub-basins of the central Baltic Sea, highlighting the general complexity.

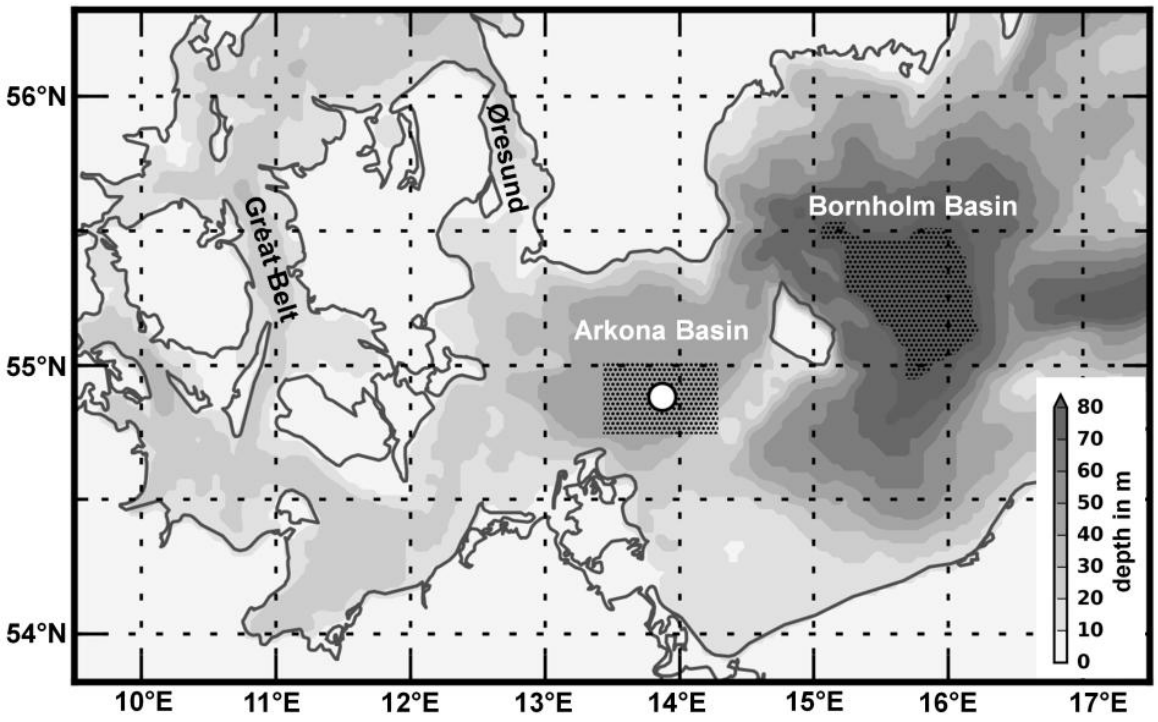

Figure 2: Detailed map of the south-western Baltic Sea. The white dot indicates the location of the observational platform in the Arkona Basin. Areas selected for vertically resolved hydrodynamic model data are depicted in shaded areas around the platform and additionally in the Bornholm Basin. Bathymetric data taken from the hydrodynamic Kiel Baltic Sea Ice-Ocean Model described in e.g. [26].

Major inflows into the Baltic usually take place in the period from August to April and in 60% of the cases between November and January [25]. During recent decades larger inflow events were less frequent. Minor inflow events, however, were recorded regularly [26], which had a positive effect on the reproductive volume sustaining egg development in the Bornholm Basin. The improvements of the oxygen-related spawning conditions, however, often did not persist to the end of the spawning season in August, and the reproductive volume returned quickly again to low levels in the middle of the summer [27].

Standard advice on fishing opportunities and catch of Eastern Baltic cod is based on yearly stock assessments and short-term population forecasts, not including any environmental considerations [8,28]. A major obstacle preventing the use of environmental data in stock assessment is the necessity for in time and regularly available information, which can in most cases not be guaranteed on the basis of e.g. ship based investigations. Stock assessment efforts are usually started in March each year when environmental data of the current year are simply not yet available, because compiling and checking data is time consuming. Within the Baltic Sea collective data base for oceanographic measurements at ICES, data is usually available with a lag of 2 to 4 months. Furthermore it is collected during ship cruises, which are often prevented from operating by bad weather conditions

and are performing measurements at specific time points and locations only. Therefore we examine in this study, the potential use of regular, standardized hydrographic measurements carried out on a permanently installed observational platform in the western Baltic as a short-term indicator to predict oxygen conditions during the spawning time in the Bornholm Basin.

To this end, we run a hydrodynamic ocean model setup to hindcast in detail the salinity conditions in the Arkona Basin and oxygen conditions in the Bornholm Basin for the last 40 years to be used for the analysis. Salinity measurements at the observational platform were only started from 2002 and actual measurement data, from e.g. the ICES Oceanographic data base, is also not available in a sufficient coverage of the last 40 years to make a comprehensive analysis. Therefore using the model data, we first investigate the general correlations between salinity conditions in the Arkona Basin (western Baltic Sea) and oxygen conditions in the Bornholm Basin. Furthermore we analyse the predominant development of the oxygen content in the Bornholm Basin during the spawning season and demonstrate that oxygen conditions generally decline after the inflow season, and that the oxygen condition for April, the beginning of the spawning season, is an excellent indicator for the egg survival probability during the entire annual reproductive cycle. Finally, we determine a functional relationship between salinity conditions in the Arkona Basin and oxygen conditions as well as cod egg survival probability in the Bornholm spawning ground for eggs spawned by different age-classes of female cod.

Materials and Methods

Measurement platform

The mentioned permanently installed measurement platform was newly deployed with a semi-submersible floating platform in 2002 by the Leibniz Institute for Baltic Sea Research, Warnemünde (IOW) on behalf of the Federal Maritime and Hydrographic Agency (BSH) and is also maintained by IOW on behalf of the BSH. It is situated in the Arkona Basin at the position of 54°53' N, 13°52' E (Fig 2) and is part of the automated German marine monitoring network in the North Sea and Baltic Sea (MARNET). The maintenance of the platform is scheduled for at least six visits per year. In case of malfunction or damages the number of visits is increased. At the beginning and at the end of the maintenance CTD measurements are conducted. These measurements are used to identify and correct data drifts.

The platform is equipped with a set of hydrographic sensors measuring temperature and salinity that are placed in 8 different depths between 2 and 43m (specifically 2, 5, 7, 16, 25, 33, 40 and 43 m). Two of which are also equipped with an oxygen sensor. The station transmits hourly real-time data ashore. This transmission uses Meteosat as well as the Global System for Mobile Communications (GSM). Data is undergoing a real time quality control that is agreed in the CMEMS in situ TAC for all European monitoring stations (CMEMS= Copernicus Marine Environment Monitoring Service; In situ TAC= in situ Thematic Assembly Center; A description of the quality control procedures can be downloaded from: http://marine.copernicus.eu/documents/QUID/CMEMS-INS-QUID-013-030-036.pdf). Data is made freely available under the Copernicus Service (for

registered users) or by request from the BSH. It is also available in a delayed mode with an enhanced quality control. This enhanced quality control comprises of an additional comparison against a climatology and visual inspection, delaying the data availability by one month.

To include a succession of several inflow and stagnation periods in the analysis and with that produce more reliable functional relationships between the Arkona Basin salinity and the spawning conditions for Eastern Baltic cod in the Bornholm Basin, we aimed at using a dataset at least covering several decades. Therefore other sources of data than the Arkona Station platform established in 2002 were needed.

Data source for the analyses

As a preliminary test in situ abiotic data taken from the ICES hydrological data base was downloaded (available at http://ocean.ices.dk/HydChem) [29], averaged with monthly resolution in 5m depth intervals and tested for their applicability in this study. Unfortunately especially for the winter period from November to February, available coverage was not sufficient. For the depth layer 30-35m within the area chosen around the platform (Fig 2), for example, data is available for the months December and January only in 10% and 30% of the years between 1971 and 2013, respectively. Moreover, in most cases when data is available, it consists of snapshots, i.e. only one or two data points per month. Reasons could be the prevailing weather conditions during this period and generally a higher interest in more biological active seasons. The spatially and temporally highly variable salinity environment in the Arkona Basin is not sufficiently represented by this data to perform a comprehensive analysis. The derived relationships could not be applied to hourly measured data from the Arkona observation platform. A solution to this problem is offered by using hydrographic data simulated by numerical ocean model setups, which were used instead for the analyses in this study. The advantage is the high spatial and temporal resolution, and results have been shown to be in very good agreement with field observations in terms of simulating average conditions and interannual variations. Lehmann et al. [26] showed that the mean and natural variability range is well captured by the model and stated that the correspondence between two individual CTD profiles and the profiles produced by the model for the same locations and time points were very high. The simulated conditions provide a “quasi-synoptic” view on the environmental dynamics at discrete locations and the compiled salinity and oxygen data sets can be used for a comprehensive analysis of characteristics of the ecosystem.

Therefore the basis for our analysis was chosen to be the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM) [30,31]. The horizontal resolution of the coupled sea ice–ocean model is at present 2.5 km. In the vertical 60 levels are specified, which enables the upper 100 m to be resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, Kattegat and Skagerrak. At the western boundary, a simplified model of the North Sea is connected to the Baltic model domain to provide characteristic North Sea water masses entering the domain. The oxygen conditions in the entire Baltic Sea are described by an oxygen consumption sub-model coupled to BSIOM [26]. It describes one pelagic, one benthic and one sediment oxygen sink, and consumption rates are calculated based on temperature and oxygen [32], where rates are higher at higher temperatures and rates are

lower at lower oxygen levels. The coefficients of the oxygen model were originally developed for the transition region between North Sea and Baltic Sea. As primary production in the Baltic Sea is smaller, oxygen consumption rates are scaled for each sub-basin relative to the Kattegat and Belt Sea. Furthermore, to account for long-term changes in oxygen consumption from i.e. eutrophication, rates are further scaled to include trends in primary production [26].

The model is forced by low frequency sea level variations in the North Sea/Skagerrak region calculated from the BSI (Baltic Sea Index) [31,33]. For this study two model setups have been used that differ in the atmospheric forcing. The first setup is forced by the Swedish Meteorological and Hydrological Institute (SMHI) meteorological database (Lars Meuller, pers. comm.) which for the period 1970—2010 covers the whole Baltic drainage basin. The second setup is forced by ERA-Interim reanalysis fields [34] that allow with regular updates until the present for a simulation of the period since 1979. The first model setup was run for the period 1970—1979, the second for the period 1979—2015. Hydrographic profiles were extracted in daily resolution.

Two series of hydrographic profiles with information on salinity and oxygen were extracted from the model output. This was done by averaging each depth layer over the two areas shown in Fig 2, representing the area around the observational platform in the Arkona Basin and the part of the Bornholm Basin with a water depth >70m. The temporal resolution was decreased for the analyses to a monthly resolution. The resulting monthly profiles in the vertical model resolution of 3 m for both areas were used to investigate correlations between salinity in the Arkona Basin and oxygen in the Bornholm Basin (Analysis #1). The Bornholm Basin profiles were further averaged within two integrated depth layers below the halocline to test for a functional relationship for water depths relevant for cod reproduction (Analysis #3). Moreover the profiles for the Bornholm Basin were interpolated in regard to water density (egg buoyancy) to investigate the seasonal development of the spawning conditions (Analysis #2), as well as the functional relationship between salinity in the Arkona Basin and the spawning conditions at 3 specific density layers relevant for cod reproduction (Analysis#3).

Arkona Basin salinity to Bornholm Basin oxygen correlations (Analysis #1)

We first focused on the correlations of salinity in the Arkona Basin with oxygen in the Bornholm Basin. Used were those time periods with the majority of Baltic inflow situations (November to January) extended by two months to March. In that way we included data up to the start of the Eastern Baltic cod spawning season in April [12,35,36]. To analyse large-scale influences of Baltic inflow events, all data of the Bornholm Basin below 50 meters was included and correlations were performed for lags up to 2 months for the period 1971 – 2015. The vertical resolution of the used profiles corresponded to the vertical resolution of the BSIOM of 3 m layers. Before applying cross-correlation statistics in between time series for each month and depth level, they were linearly detrended, checked for autocorrelation by the Ljung-Box [37] and Durbin-Watson tests [38]; and reduced to the residuals of an AR model fit of increasing order until the tests results were negative. In the following correlations in between the resulting time series of salinity and oxygen the strongest correlations were found for the 33m level in the Arkona Basin. The

subsequent analyses were therefore based only on the Arkona Basin salinity at this depth level, and tested for a dependency of the environmental conditions within the Bornholm Basin on the salinity levels within the Arkona Basin (Analysis #3 and Example).

Temporal development of the oxygen content in the Bornholm Basin during the spawning season (Analysis #2)

To investigate the seasonal oxygen development following the inflow period in the spawning habitat of cod, the model data was used to assemble monthly mean values of oxygen content in the Bornholm Basin on different buoyancy levels by interpolation in regard to density (1009, 1011, 1013 kg m^{-3}, corresponding to a salinity of ca. 11, 13.5 and 16 at a temperature of around 5°C). These levels were chosen to represent the buoyancies of eggs of different female age categories: old (large), mid-age (medium size) and young (small) cod, and were based on the results described in Vallin and Nissling [39]. Oxygen time series at all buoyancy levels for April were compared to the time series found for August to determine the common direction of the seasonal oxygen development. Furthermore the integral of the oxygen concentration between May and August on all buoyancy levels was calculated for each year. With that, the dependency of the oxygen concentration during the entire spawning season on the initial value in April could be investigated. Tests were performed with linear correlation statistics between the mean value in April as independent variable and the integral from May to August as dependent variable. The 1013 kg m^{-3} density level did not exist in the Bornholm Basin in 15 of the 44 years due to overall low salinity (density) levels in the Basin and in 3 of the remaining years the density layer disappeared in between June and August. All of these were excluded from the correlation.

Arkona Basin salinity predicting Bornholm Basin oxygen and Eastern Baltic cod egg survival (Analysis #3)

To investigate the functional relationship between salinity measurements at 33 m in the Arkona Basin and the oxygen content in the spawning habitat of Eastern Baltic cod, we averaged oxygen concentrations in the Bornholm Basin within two layers. The first one with the range between 50 and 70 m broadly represents the floating range of eggs of older, repeat spawners. The second one (70 to 95m depth) represents the depth of occurrence of eggs spawned by young females [39,40]. We selected from the averaged time series the oxygen values for April as dependent variable. April represents the beginning of the spawning season of cod and analysis #2 showed that the oxygen conditions in the remaining spawning season depend on this initial content. As independent variable we used maximum salinity values at the 33m depth layer in the Arkona Basin between January and March. The monthly mean salinity here represents a measure of intensity of the water inflow from the Kattegat and the time period was identified as most influential by analysis #1. The capabilities of the found relationship for operational forecasting was tested by the method of leave one out cross validation.

Furthermore, we used the modelled data on oxygen concentration to calculate the potential egg survival probability in the Bornholm Basin, which is based on a modelled egg survival function obtained from experimental data [13]:

$$y_o = 100((1 - e^{-0.71x})^{11.63}), \quad (1)$$

where y_o is the oxygen-dependent survival probability before hatch and x is the oxygen content in ml l^{-1}. The function (r^2 = 0.94) describes a sigmoid curve with almost total mortality at 2 ml l^{-1} oxygen content, ~50% mortality at 4 ml l^{-1}, and <10% mortality at 7 ml l^{-1}.

To take cod stock structure into account, we assembled model data time series on oxygen-related egg survival probability for the same buoyancy levels (1009, 1011, 1013 kg m^{-3}) as described above. The derived values for April each year were then used for a correlation with the maximum salinity value in the Arkona Basin at 33 m between January and March similar as the oxygen data from the two coarser depth layers of 50 to 70 and 70 to 95 m before. Also here the capabilities for operational forecasting of the found relationships was tested by leave one out cross validation.

Exemplary daily interval time series from the measurement station

To give an example of the potential direct applicability of real time measurements transmitted by the observational platform in the Arkona Basin, we finally present as proof of concept records of salinity measurements from the station together with the oxygen concentration data in the Bornholm Basin from the BSIOM. We increased the temporal resolution for this exercise to a daily interval to keep more of the available resolution of the data transmitted from the measurement station and to emphasise on the rapid fluctuations of salinity in the area. We also added monthly means to connect such "real time" daily measurements to the functional relationships developed before. Furthermore we chose a period with a pronounced major Baltic Inflow, as represented by the winter months in 2014/15 to show the propagation of the inflow between the two locations and exemplary applied the functional relationships to predict the oxygen concentration in the Bornholm Basin at the beginning of April and the associated egg survival probabilities for mid-age and young females.

Results

Monthly averaged profiles obtained from hydrodynamic model runs were used to study the long-term variability (1971 to 2015) of the Eastern Baltic cod spawning environment. A close coupling of salinity data from the Arkona Basin with the oxygen concentrations below the halocline in the Bornholm Basin was found by using cross-correlation statistics with detrended time series. Fig 3 shows the cross correlations between salinity at the 33m depth level in the Arkona Basin and the oxygen concentrations in different depths in the Bornholm Basin. Investigated time lags for the oxygen time series in the cross-correlations with the salinity time series in November, December, January and February, were selected as 0,1 and 2 months. Positive correlations are indicative of the chronology and the predominant offset point of an increase in the amount of imported saline, oxygen-rich North Sea water. Salinity values in November and December were found not to be useful

in any of the time lags for predictions of oxygen levels in the Bornholm Basin with r < 0.3 and low significant levels. The highest significant correlations were found to occur for the 33m salinity level in the Arkona Basin in January and the oxygen content in the Bornholm Basin at depth levels below 72m in February (Fig 3, 0.5 < r < 0.6; p<0.001). But also salinity in February and oxygen conditions in March showed significant correlations of 0.4 < r < 0.5 for depth layers below 75m. Significant positive cross-correlations were also found for February salinity values and oxygen values in March below 69m (0.4 < r < 0.6; p<0.01). Weaker correlations between salinity values in March and oxygen conditions in April and May were also present with 0.3 < r < 0.4 but less significant (p <0.05).

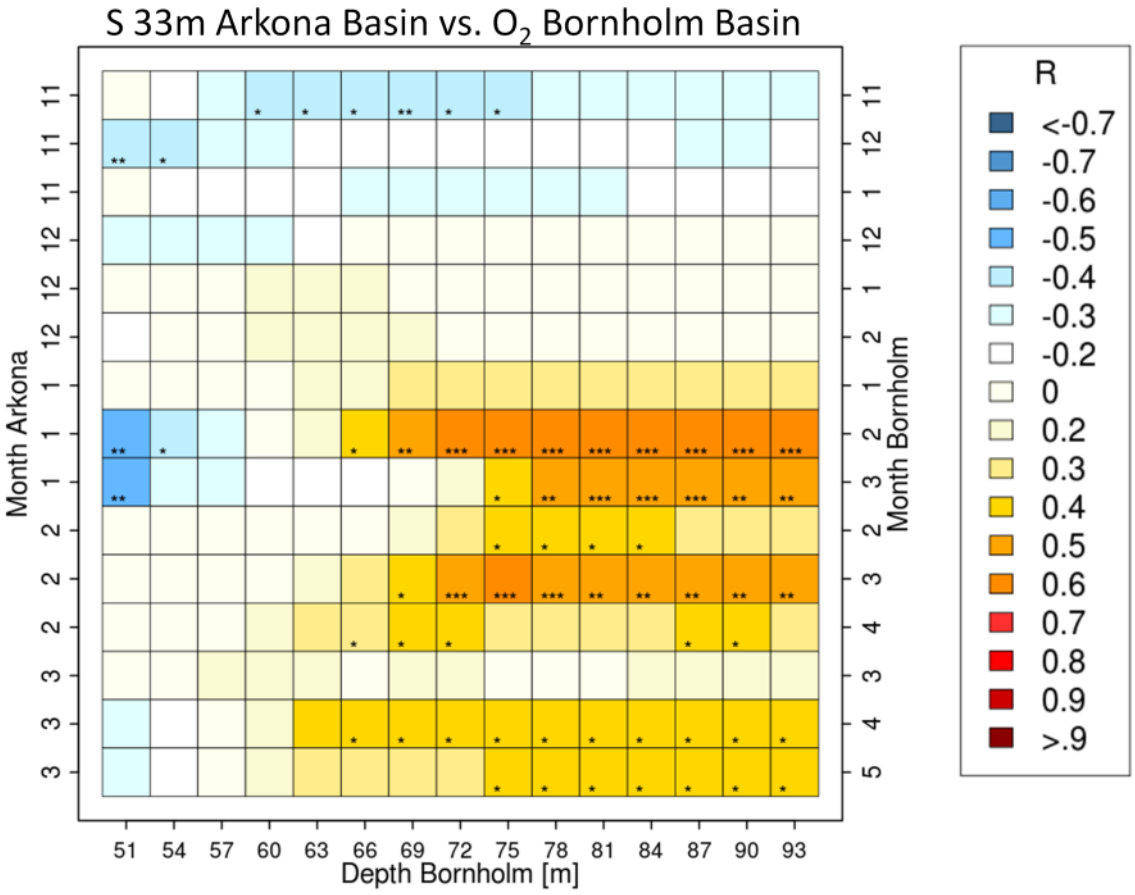

Figure 3: Correlation coefficients of salinity at 33m depth for different months in the Arkona Basin vs. oxygen concentration at various depths for successive months in the Bornholm Basin. Time series of monthly mean values for the correlations were taken from hydrodynamic model runs (BSIOM) hindcasting the period 1970-2015. From the entire period November to March salinity values at the 33m depth level in the Arkona Basin were correlated respectively to the vertical oxygen distribution in the Bornholm Basin between November and May. The value of the correlation coefficient is depicted in colour code for each combination of months selected for salinity and oxygen values and additionally the corresponding depth layer in the Bornholm Basin. The significance of each correlation is depicted with asterisks as follows: p>0.05 = no asterisk, p<0.05 = *, p<0.01 = **, p<0.001 = ***.

These results demonstrate a correlative link within the inflow season between salinity in the Arkona Basin and oxygen concentration in the Bornholm Basin a few weeks later. Fig 4 shows that there are large interannual variations in the prevailing oxygen conditions in the Bornholm Basin at the beginning of the spawning season but with the common feature

of decreasing concentrations from April to August (in 91% of cases). Eggs spawned by old repeat spawners floating around the 1009 kg m^{-3} density level inhabit a less variable habitat in April (5 - 9 ml/l O_2; Fig 4 top panel) than the ones spawned by young females which are neutral buoyant at 1013 kg m^{-3} (0.5 – 8 ml/l O_2; Fig 4 bottom panel). Regressions between the April oxygen content and the integrated oxygen content over May to August (Fig 5 and Table 1) quantify moreover that the overall oxygen conditions throughout the whole spawning season are depending on the prevailing oxygen level in April. For all the density levels strong correlations were obtained (Adj. R^2 = 0.48 – 0.95) with only the estimation of the intercept parameter for the 1013 kg m-3 level showing a none-significant p value of 0.6. Overall these results indicate that the processes determining the spawning season's oxygen conditions for cod are mostly completed upon April, confirming results from Hinrichsen et al (Fig 7 in [40]). This also justifies the chosen limitation of the analyses to the months November to April.

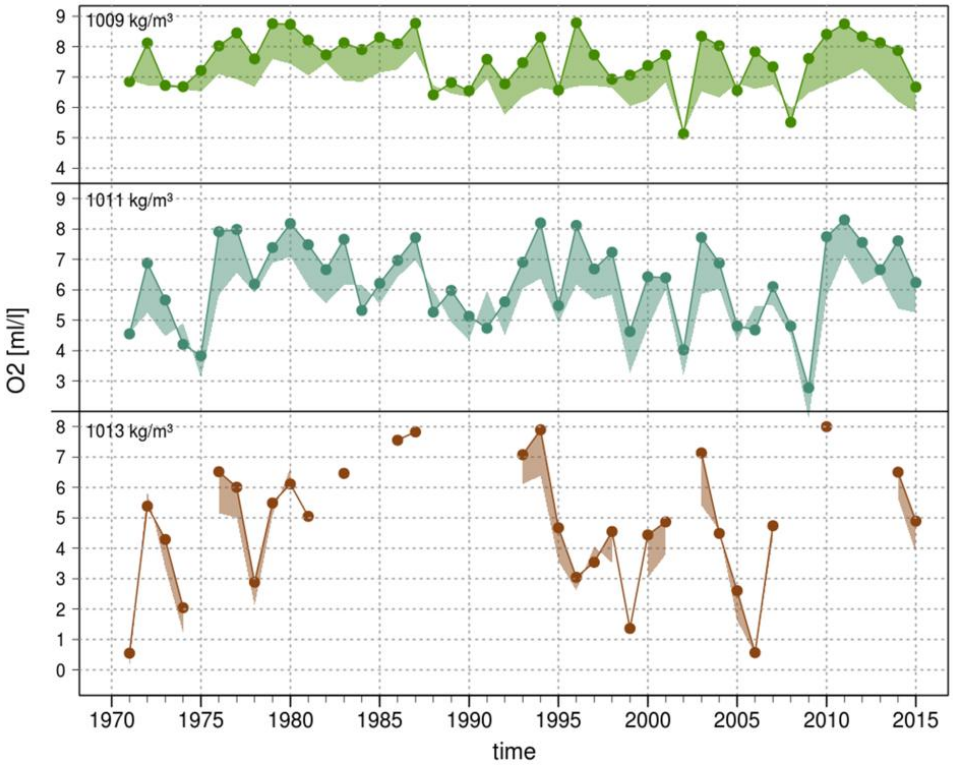

Figure 4: Oxygen concentration time series for the Bornholm Basin on neutral egg buoyancy levels for the period 1971-2015. The density levels represent neutral buoyancy of Eastern Baltic cod eggs spawned by old (1009 kg m^{-3}, top panel), middle aged (1011 kg m^{-3}, middle panel), or young females (1013 kg m^{-3}; bottom panel), respectively. Dots and solid lines represent monthly mean values in April of the years 1971-2015 and shaded areas the differences to the monthly mean values in August of the same year. Data was taken from hydrodynamic model runs (BSIOM).

As a next step, we tested for a functional relationship between salinity in the Arkona Basin at 33m depth and the spawning conditions for Eastern Baltic cod in the Bornholm Basin. In the first part of analysis #3 involving oxygen, we separated two depth layers: the range between 50 and 70 m broadly represents the floating range of eggs of older, repeat spawners; The second one (70 to 95m depth) represents the depth of occurrence of eggs spawned by young females. From both series the mean oxygen content in April was

correlated to the maximum of the monthly mean salinity values in the Arkona Basin between January and March. For the upper level no correlation was found, while for the lower level a significant correlation was obtained (Adj. $R^2 = 0.41$, $p < 0.001$; Fig 6a; Table 2). The standard residual error of the overall fit was found to be 1.31 and the cross validation mean test error was calculated as 1.8.

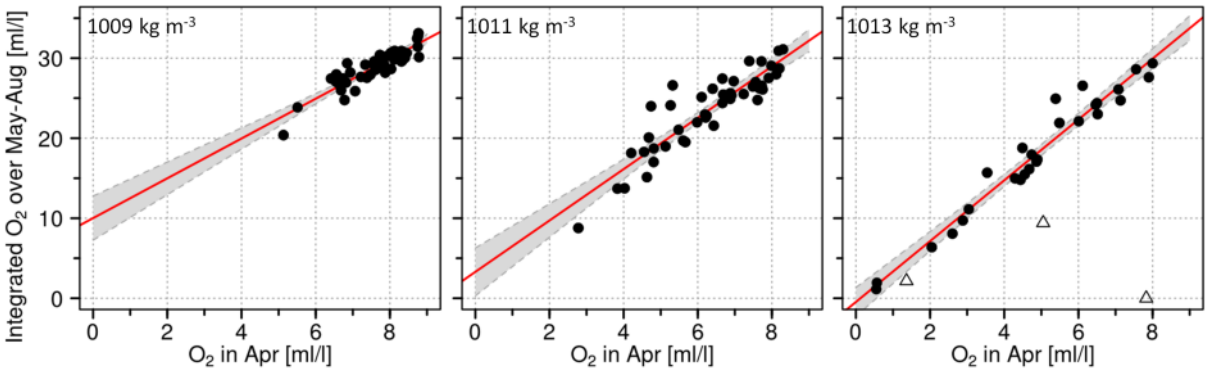

Figure 5: Oxygen content relationships in the Bornholm Basin on neutral egg buoyancy levels between the beginning (April) and the rest of the spawning season (Integral May-Aug). Monthly means of the oxygen content on 3 density levels in the Bornholm Basin derived from hydrodynamic model runs (BSIOM) hindcasting the period from 1971 until 2015 were used for the analysis. The density levels represent neutral buoyancy of eggs spawned by old (1009 kg m-3, left panel), middle aged (1011 kg m-3, middle panel), and young females (1013 kg m-3, right panel), respectively. Linear regression lines are shown in red and the 95% confidence intervals as gray shaded areas. Regression parameters are shown in Table 1. Δ = represents years in which the density layer did not exist for the entire spawning season.

Table 1: Statistical parameters of linear regressions shown in Fig 5

Monthly mean oxygen content in the Bornholm Basin [ml/l]:
April vs. Integral over May to August

*Density level **1009 kg m^{-3}** (Fig 5 left panel):*

Rsqr	Adj Rsqr	Standard Error of Estimate		
0.8169	0.8127	1.026		
Parameter	**Coefficient**	**Std. Error**	**t**	**p**
Intercept	10.01	1.3686	7.314	< 0.001
Slope	2.4866	0.1795	13.852	< 0.001

*Density level **1011 kg m^{-3}** (Fig 5 middle panel):*

Rsqr	Adj Rsqr	Standard Error of Estimate		
0.819	0.48148	2.123		
Parameter	**Coefficient**	**Std. Error**	**t**	**p**
Intercept	3.2948	1.484	2.22	0.0317
Slope	3.2091	0.230	13.95	< 0.001

*Density level **1013 kg m^{-3}** (Fig 5 right panel):*

Rsqr	Adj. Rsqr	Standard Error of Estimate		
0.9534	0.9525	1.725		
Parameter	**Coefficient**	**Std. Error**	**t**	**p**
Intercept	-0.464	0.8795	-0.528	0.602
Slope	3.7991	0.1662	22.859	<0.0001

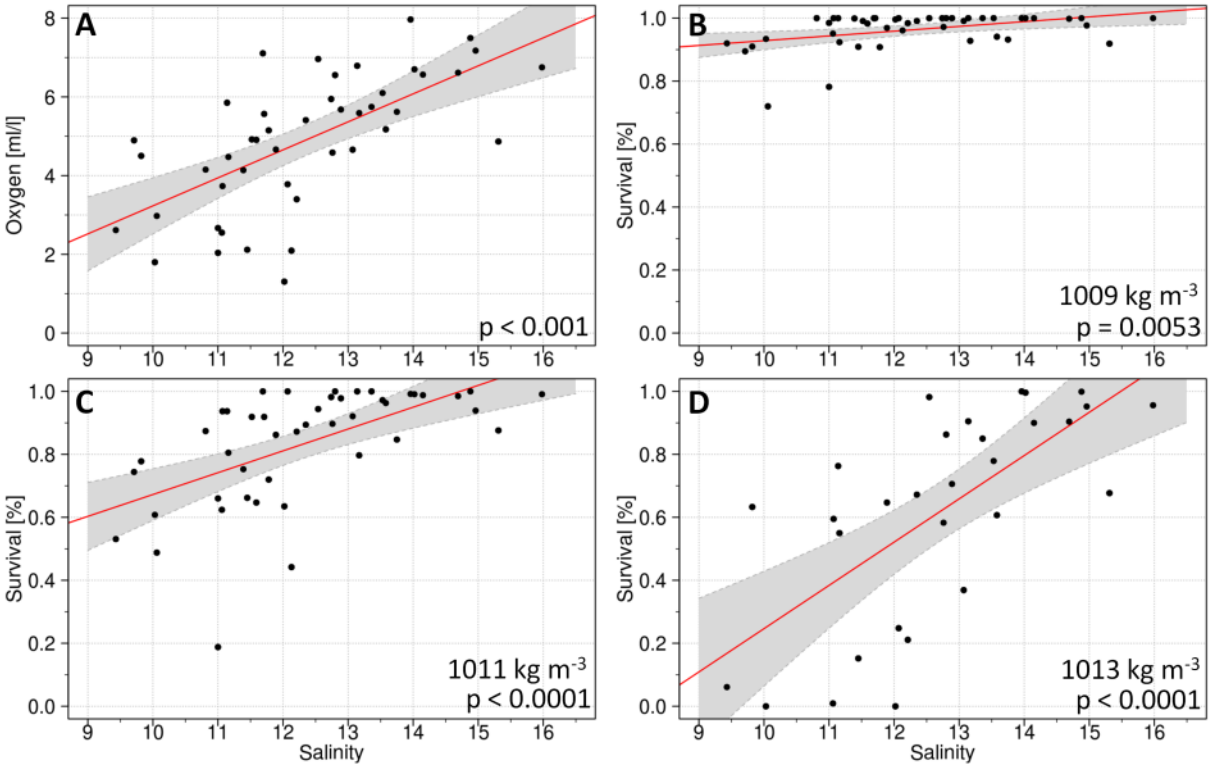

Figure 6: Correlations of monthly mean salinity values in the Arkona Basin at 33m depth vs. oxygen content and oxygen-related egg survival in the Bornholm Basin. The explanatory variable in all panels is the maximum monthly mean salinity value between January and March at the 33m depth level in the Arkona Basin for the years 1971 to 2015. As dependent variables the mean oxygen condition and oxygen related egg survival probabilities in the Bornholm Basin in April of the same year were chosen. Panel A shows the linear correlation to the mean oxygen content in the depth range from 70 to 95m; B, C and D, the correlations to the oxygen-related Eastern Baltic cod egg survival probability at the egg neutral buoyancy level 1009, 1011 and 1013 kg m^{-3}, respectively. Linear regression lines are shown in red and the 95% confidence intervals as gray shaded areas.

Table 2: Statistical parameter and cross validation results of the linear functions shown in Fig 6.

Maximum Salinity Jan. to Mar. Arkona Basin 33m [psu] vs. oxygen content [ml/l] Apr. Bornholm Basin 70-95m (Fig 6A):

Rsqr	Adj Rsqr	Std. error residuals	F	p	d.f.
0.4236	0.4102	1.31	31.6	<0.001	43

Parameter	Coefficient	Std. Error	t	p
y_0	-3.8837	1.5741	-2.467	0.0177
slope	0.7114	0.1266	5.621	<0.0001

Cross validation results

Mean Rsqr	Std. deviation	Mean training error	95% conf. int.	Mean test error	95% conf. int.
0.4237	0.0156	1.638	0.1103	1.758	5.023

Maximum Salinity Jan. to Mar. Arkona Basin 33m [psu] vs. oxygen-related egg survival Apr. Bornholm Basin buoyancy level 1009 [kg m^{-3}] (Fig 6B):

Rsqr	Adj Rsqr	Std. error Residuals	F	p	d.f.
0.1674	0.148	0.0532	8.643	0.0053	43

Parameter	Coefficient	Std. Error	t	p
y_0	0.777	0.064	12.15	<0.0001
slope	0.015	0.005	2.94	0.0053

Cross validation results

Mean Rsqr	Std. deviation	Mean training error	95% conf. int.	Mean test error	95% conf. int.
0.1675	0.0126	0.0027	0.0004	0.003	0.0169

Maximum Salinity Jan. to Mar. Arkona Basin 33m [psu] vs. oxygen-related egg survival Apr. Bornholm Basin buoyancy level 1011 [kg m^{-3}] (Fig 6C):

Rsqr	Adj Rsqr	Std. error residuals	F	p	d.f.
0.346	0.331	0.1505	22.75	<0.0001	43

Parameter	Coefficient	Std. Error	t	P
y_0	-0.0211	0.1808	-0.117	0.907
slope	0.0694	0.0145	4.770	<0.0001

Cross validation results

Mean Rsqr	Std. deviation	Mean training error	95% conf. int.	Mean test error	95% conf. int.
0.3464	0.0136	0.0216	0.0023	0.0235	0.1054

Maximum Salinity Jan. to Mar. Arkona Basin 33m [psu] vs. oxygen-related egg survival Apr. Bornholm Basin buoyancy level 1013 [kg m^{-3}] (Fig 6D):

Rsqr	Adj Rsqr	Std. error residuals	F	p	d.f.
0.459	0.4395	0.2504	23.74	<0.0001	28

Parameter	Coefficient	Std. Error	t	p
y_0	-1.1279	0.36143	-3.121	0.0042
slope	0.1374	0.02821	4.872	<0.0001

Cross validation results

Mean Rsqr	Std. deviation	Mean training error	95% conf. int.	Mean test error	95% conf. int.
0.4590	0.0235	0.0584	0.0048	0.0671	0.1480

For the second part of analysis #3 involving oxygen-related egg survival, we further refined the vertical resolution but kept the setup of correlating the values of the dependent variable in April to the maximum of the monthly mean salinity level in the Arkona Basin at 33m between January and March. Survival probability was calculated at three buoyancy/density levels of 1009, 1011 and 1013 kg m^{-3} representing levels of neutral buoyancy of eggs spawned by old, mid-age and young females, respectively. The results for the density layers showed significant differences (Fig 6; Table 2). Survival of eggs spawned by old females were almost independent on the 33m salinity level in the Arkona Basin with an adj. R^2 of 0.15, while the survival probability for eggs spawned by mid-age and young females could be related to the salinity level in the Arkona Basin with adj. R^2 of 0.33 and 0.44, respectively. These correlations were also found highly significant with p values < 0.0001 on 43 and 28 degrees of freedom. The mean test errors of the performed leave one out cross validation resulted in 0.024 and 0.067; and the residuals of the overall fit to the data had a standard error of 0.053 and 0.151 for the 1011 and 1013 kg m^{-3} density level, respectively.

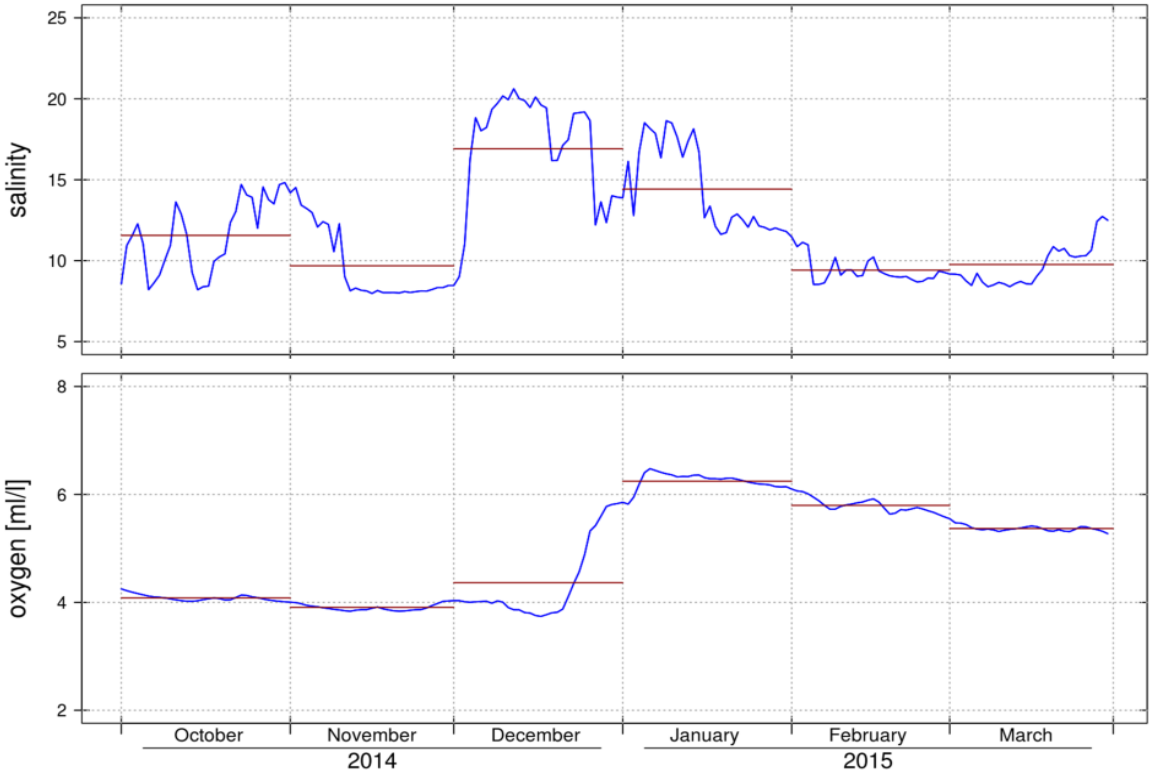

Figure 7: Comparison of measured salinity at 33m from the Arkona Basin and oxygen content in the Bornholm Basin from modeled data. Time series of salinity measured at the 33m depth level (Arkona Basin platform) operated by the Federal Maritime and Hydrography Agency, Hamburg, Germany is shown in daily resolution in the upper panel. Lower panel represents vertically mean oxygen concentration data (averaged between 60 and 90m) of the Bornholm Basin taken from the hydrodynamic model runs (BSIOM). Monthly means are indicated as horizontal lines.

An example to demonstrate how routinely performed measurements in the western Baltic Sea could be utilised for the short-term prediction of the Eastern Baltic cod spawning environment is shown in Fig 7. The combination of salinity data (daily interval and monthly averages) measured at the 33m level in the Arkona Basin with the average oxygen concentration below the halocline in the Bornholm Basin taken from the hydrodynamic

model showed, that the major Baltic inflow at the end of 2014 [17] was observed in the Arkona Basin in December (mean S in December = 16.91), while the improvements of the oxygen concentration within and below the halocline (60, 75 and 90m) in the Bornholm Basin occurred around 3 weeks later (mean oxygen in January = 6.24 ml/l). The developed functional relationships, however, do have the requirement to use the maximum of the monthly mean salinity from the Arkona Basin between January and March. Therefore using the monthly mean salinity for January of 14.42 and the relationships presented in Table 2 the oxygen content in the 70-95m depth layer in the Bornholm Basin of 6.37 ± 0.66 ml/l is predicted for April. The data derived from the BSIOM setup resulted in a monthly mean of 5.33 ml/l for this month and water layer. This deviation is well inside of the functional capacity of the relationship tested by cross validation (mean test error of 1.6; Table 2). Furthermore for the spawning season of 2015 the egg survival probabilities for eggs spawned by young and mid-aged females would have been predicted to be exceptionally good with 68-100 % and 89-100%, respectively.

Discussion

In this study we investigated the possibility of predicting the Eastern Baltic cod spawning environment based on salinity measurements from a permanently installed monitoring platform located in the western Baltic Sea. We identified the salinity in the Arkona Basin at 33 m depth level as good short-term indicator for the oxygen conditions in the Bornholm Basin. Although inflow events were recorded frequently also in November and December [21], we identified for the last 40+ years the months January to March as most influential for the oxygen conditions in the Bornholm Basin. Baroclinic inflows during the summer were regularly observed from 1996 on [41] and could become more frequent in the future [1], but our results suggest, that their impact on the spawning habitat of Eastern Baltic cod is not as strong as for major inflows occurring during the winter season. One reason could be the higher temperature of the inflowing water mass associated with less dissolved oxygen. Baroclinic inflows were suspected to extend the habitat for eggs spawned by young females in July [40], but in this study we show that the oxygen conditions in April are very good indicators of the oxygen conditions for the entire spawning season.

Direct prediction of the Eastern Baltic cod spawning environment in terms of egg survival probability from salinity measurements in the Arkona Basin at the 33 m depth level is shown here to be possible for the eggs spawned by mid-age and young females, which currently predominate the stock structure [8]. Based on the functional relationship developed in this study, egg survival probabilities would be available by the end of March each year. Old repeat spawners of the Eastern Baltic cod stock produce such large and buoyant eggs that their survival is not strongly dependent on large inflow events. Their eggs float on top of the vertical layers which could become oxygen depleted during the summer and / or stagnation years and therefore have often superior survival probabilities for their eggs than younger females. This again stresses the fact that large females do have a high value for the stocks survival and productivity [42] and efforts should be made to strengthen the larger length classes in the stock by decreasing their fishing mortality. With that the stock could be less affected by the impact of bad environmental conditions, which

reduce, as we show in this study, substantially the survival probabilities of smaller and less buoyant eggs spawned by midsized and small females.

These findings were based on data from the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM) [26], since in the preliminary analysis in-situ measurements were found not to be sufficient in resolution and temporal coverage. The relationships developed here were intended to be used with real-time data from the Arkona Basin monitoring platform, which is located in a highly variable abiotic environment, making the use of highly resolved time series unavoidable. It was chosen nevertheless due to its benefits such as being ready to use and imminent data source, which enables utilization in short-term forecasts. The hydrography and oxygen concentrations as simulated by BSIOM are in good agreement with observed variations and dynamics of the system [26]. The incorporated oxygen sub-model uses sub-basin dependent primary production rates, which are further scaled to follow observed long-term primary production development [43]. The applied consumption rates are furthermore depending on temperature and oxygen content. The sub-model extends thereby the approach of constant rates for each sub-basin, which is deemed to be already a good approximation [44]. Therefore the BSIOM is a sufficient data source to replace the in-situ measurements for use in this study and the developed functional relationships could be used in future work on incorporating an environmental factor in the Eastern Baltic cod stock assessment procedure. The relationships might have also been calculated based on coupled physical-biogeochemical models such as ERGOM [45] available for modelling hydrography and oxygen distribution in the Baltic Sea. ERGOM was shown to be a very good tool to investigate the upper mixed layer of the system, but also showed weaknesses especially in the model performance for the deep parts of the Baltic Sea sub-basins [46]. A direct comparison between different numerical model approaches is, however, missing. Moreover complex coupled physical-biogeochemical models often suffer from high levels of noise in the data, which could in turn weaken the forecasting power of derived functional relationships while the fit does not necessarily benefit from the complexity. Since the subject of this study was to find such relationships with the greatest forecasting power, the BSIOM could be a superior model choice. Nevertheless future work that aims at comparing model approaches and improving their applications for fisheries science would be beneficial.

The International Council for the Exploration of the Seas (ICES) is the main fishery advice giving body for the North-Atlantic region, including the Baltic Sea. ICES specifically acknowledged the need to develop and identify ways forward to include environmental and economic considerations in standard fishery advice [47]. For the case of the Baltic Sea fisheries, a series of working group meetings and workshops (e.g. WGIAB, WKDEICE, DEMO workshops) was held to work on Integrated Ecosystem Assessment (IEA), to be used for advice, management strategy evaluation of Baltic fish stock and science communication [8,48].

The recent history of the Baltic cod fisheries exemplifies the need to proceed on this way, and illustrates the potential value of environmental forecasting, as proposed in this paper. Both of the Baltic cod fisheries, the western as well as the Eastern cod stock fishery, suffered from dramatic quota reductions. E. g. for the western cod stock a Total Allowable

Catch (TAC) reduction of 85% was suggested in 2016 [28]. The Eastern Baltic cod fishery faced similarly hard reductions by 2015 [28]. In both cases, the timely and thoughtful inclusion of environmental information in stock assessment and advice might have attenuated the economic consequences, and maybe even buffered stock decline. Here, the early recognition of adverse environmental conditions for reproduction might serve as an early warning indicator, and hint to setting more precautionary fishing limits. By doing so, a buffer against environmentally-induced reductions in stock productivity might be created.

Here, we show that suitable data are already collected on a regular basis. For short-term predictions the existing observational platform can be used. Periods of increased salinity at the 33m level within the winter months can be identified and with the relationships shown in this study an estimation be made of the seasonal egg survival probability spawned by the predominant size classes within the stock, as presented exemplarily for the inflow year 2014/15. In a similar manner data of particularly low salinities from the Arkona Basin would result in very low egg survival probabilities that could be taken as an early warning indicator for a lowered reproductive success, with its impact on the cod stock structure during the following years. This offers a cost-neutral way of informing stock assessment of Eastern Baltic cod, proceeding on the way to more integrated advice. Advice finding efforts usually start in April / May each year. Our results give the opportunity to include environmental information about the entire following spawning season to this time already, where as monitoring cruises by ship and direct measurements give complete information only in hindsight when assessment calculations are already in an advanced state. As discussed during relevant ICES workshops (e.g. WKDEICE) [48] such information might be used in different ways to inform stock assessment and advice [49]:

1. Using an environmentally-sensitive stock-recruitment function in the short-term forecast of the current standard procedure;
2. Using all relevant information from an environmental assessment to modify fishing mortalities in short-term forecast; depending on the state and trend in environmental conditions, F-multiplier could be used, allowing for increased or decreased fishing opportunities, respectively;
3. Fishing mortality (F)-multipliers could be directly used in the advice giving process, reflecting environmental assessment outcomes.

The utilisation of salinity as relatively simple indicators allows a general examination, how the environmental conditions affect Baltic cod egg development and survival, and is relatively inexpensive compared to field observations. Investigating and deciding, however, how to include proxies of stock productivity into the advice finding process is outside of the scope of this study. Modifications of recruitment models and sections of population analyses within the assessment incorporating our findings and also other possibilities on the way towards an environmental integrated advice need to be subject to future studies.

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References (Chapter 4)

1. Team BA. Assessment of climate change for the Baltic Sea basin: Springer Science & Business Media; 2008.
2. Cardinale M, Casini M, Arrhenius F, Håkansson N. Diel spatial distribution and feeding activity of herring (Clupea harengus) and sprat (Sprattus sprattus) in the Baltic Sea. Aquatic Living Resources. 2003;16(3):283-92.
3. Möllmann C, Kornilovs G, Fetter M, Köster FW, Hinrichsen HH. The marine copepod, Pseudocalanus elongatus, as a mediator between climate variability and fisheries in the Central Baltic Sea. Fisheries Oceanography. 2003;12(4-5):360-8. doi: 10.1046/j.1365-2419.2003.00257.x. PubMed PMID: WOS:000185446000014.
4. Voss R, Peck MA, Hinrichsen H-H, Clemmesen C, Baumann H, Stepputtis D, et al. Recruitment processes in Baltic sprat–A re-evaluation of GLOBEC Germany hypotheses. Progress in Oceanography. 2012;107:61-79.
5. Baumann H, Hinrichsen H-H, Möllmann C, Köster F, Malzahn A, Temming A. Recruitment variability in Baltic Sea sprat (Sprattus sprattus) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. Canadian Journal of Fisheries and Aquatic Sciences. 2006;63(10):2191-201.
6. Blenckner T, Llope M, Möllmann C, Voss R, Quaas MF, Casini M, et al. Climate and fishing steer ecosystem regeneration to uncertain economic futures. Proceedings of the Royal Society B: Biological Sciences. 2015;282(1803).
7. Möllmann C, Blenckner T, Casini M, Gardmark A, Lindegren M. Beauty is in the eye of the beholder: management of Baltic cod stock requires an ecosystem approach. Marine Ecology Progress Series. 2011;431:293-7. doi: 10.3354/meps09205. PubMed PMID: WOS:000291953100024.
8. Karpushevskaia A, Nielsen A, Mikhaylov A, Luzenczyk A, Florin A-B, Albert A, et al. Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 12-19 April 2016, ICES HQ, Copenhagen, Denmark. International Council for the Exploration of the Sea; 2016.
9. EU 2010/477/EU: Commission Decision of 1 September 2010 on criteria and methodological standards on good environmental status of marine waters (notified

under document C(2010) 5956) Text with EEA relevance. OJ L 232, 2.9.2010, p. 14–24, section 3.2.

10. Voss R, Quaas M, Schmidt J, Hoffmann J. Regional trade-offs from multi-species maximum sustainable yield (MMSY) management options. Marine Ecology Progress Series. 2014;498:1-12.
11. Dutil JD, Brander K. Comparing productivity of North Atlantic cod (Gadus morhua) stocks and limits to growth production. Fisheries oceanography. 2003;12(4- 5):502-12.
12. Bagge, O., Thurow, F., Steffensen, E., and Bay, J. 1994. The Baltic cod. Dana, 10: 1–28
13. Köster FW, Möllmann C, Hinrichsen HH, Wieland K, Tomkiewicz J, Kraus G, et al. Baltic cod recruitment - the impact of climate variability on key processes. Ices Journal of Marine Science. 2005;62(7):1408-25. doi: 10.1016/j.icesjms.2005.05.004. PubMed PMID: WOS:000233659300021.
14. Köster FW, Hinrichsen H-H, St. John MA, Schnack D, MacKenzie BR, Tomkiewicz J, et al. Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Canadian Journal of Fisheries and Aquatic Sciences. 2001;58(8):1534-56.
15. Köster FW, Huwer B, Hinrichsen H-H, Neumann V, Makarchouk A, Eero M, et al. Eastern Baltic cod recruitment revisited—dynamics and impacting factors. ICES Journal of Marine Science. 2016;74(1):3-19.
16. Eero M, Köster FW, Plikshs M, Thurow F. Eastern Baltic cod (Gadus morhua callarias) stock dynamics: extending the analytical assessment back to the mid-1940s. Ices Journal of Marine Science. 2007;64(6):1257-71. doi: 10.1093/icesjms/fsm114. PubMed PMID: WOS:000250937800018.
17. Mohrholz V, Naumann M, Nausch G, Krüger S, Gräwe U. Fresh oxygen for the Baltic Sea—An exceptional saline inflow after a decade of stagnation. Journal of Marine Systems. 2015;148:152-66.
18. Amante C, Eakins B. ETOPO1 1 arc-minute global relief model: Procedures, data sources and analysis: National Oceanic and Atmospheric Administration Technical Memorandum NESDIS NGDC-24, 19 p., doi: 10.7289. V5C8276M; 2009.
19. MacKenzie BR, Hinrichsen HH, Plikshs M, Wieland K, Zezera AS. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod Gadus morhua eggs in the Baltic Sea. Marine Ecology-Progress Series. 2000;193:143-56. doi: 10.3354/meps193143. PubMed PMID: WOS:000086115400014.
20. Plikshs M, Hinrichsen HH, Elferts D, Sics I, Kornilovs G, Köster FW. Reproduction of Baltic cod, Gadus Morhua (Actinopterygii: Gadiformes: Gadidae), in the Gotland Basin: Causes of annual variability. Acta Ichthyologica Et Piscatoria. 2015;45(3):247-58. doi: 10.3750/aip2015.45.3.04. PubMed PMID: WOS:000363424700004.
21. Schinke H, Matthäus W. On the causes of major Baltic inflows —an analysis of long time series. Continental Shelf Research. 1998;18(1):67-97. doi: 10.1016/S0278-4343(97)00071-X.

22. Stigebrandt A. Computations of the flow of dense water into the Baltic Sea from hydrographical measurements in the Arkona Basin. Tellus A. 1987;39(2):170-7.
23. Leppäranta M, Myrberg K. Physical oceanography of the Baltic Sea: Springer Science & Business Media; 2009.
24. Krauss W, Brügge B. Wind-produced water exchange between the deep basins of the Baltic Sea. Journal of Physical Oceanography. 1991;21(3):373-84. doi: 10.1175/1520-0485(1991)021<0373:wpwebt>2.0.co;2. PubMed PMID: WOS:A1991FC51600001.
25. Franck H. Major inflows of saline water into the Baltic Sea during the present century. Gerl Beitr Geophys. 1987;96:517-31.
26. Lehmann A, Hinrichsen HH, Getzlaff K, Myrberg K. Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. Journal of Marine Systems. 2014;134:20-8. doi: 10.1016/j.jmarsys.2014.02.012. PubMed PMID: WOS:000336349200003.
27. Hinrichsen HH, Voss R, Wieland K, Köster F, Andersen KH, Margonski P. Spatial and temporal heterogeneity of the cod spawning environment in the Bornholm Basin, Baltic Sea. Marine Ecology-Progress Series. 2007;345:245-54. doi: 10.3354/meps06989. PubMed PMID: WOS:000250195800021.
28. ICES Advice on fishing opportunities, catch, and effort Baltic Sea Ecoregion. ICES Advice 2016, Book 8, section 8.3.
29. ICES Dataset on Ocean Hydrography. The International Council for the Exploration of the Sea, Copenhagen. 2009
30. Lehmann A, Hinrichsen HH. On the thermohaline variability of the Baltic Sea. Journal of Marine Systems. 2000;25(3-4):333-57. doi: 10.1016/s0924-7963(00)00026-9. PubMed PMID: WOS:000165615100012.
31. Lehmann A, Krauss W, Hinrichsen HH. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus Series a-Dynamic Meteorology and Oceanography. 2002;54(3):299-316. doi: 10.1034/j.1600-0870.2002.00289.x. PubMed PMID: WOS:000175681000006.
32. Jonasson L, Hansen JL, Wan Z, She J. The impacts of physical processes on oxygen variations in the North Sea-Baltic Sea transition zone. Ocean Science. 2012;8(1):37.
33. Novotny K, Liebsch G, Lehmann A, Dietrich R. Variability of sea surface heights in the Baltic Sea: an intercomparison of observations and model simulations. Marine Geodesy. 2006;29(2):113-34.
34. Dee DP, Uppala SM, Simmons AJ, Berrisford P, Poli P, Kobayashi S, et al. The ERA-Interim reanalysis: configuration and performance of the data assimilation system. Quarterly Journal of the Royal Meteorological Society. 2011;137(656):553-97. doi: 10.1002/qj.828. PubMed PMID: WOS:000290450900001.
35. Wieland K, Jarre-Teichmann A, Horbowa K. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. Ices Journal of Marine Science. 2000;57(2):452-64. doi: 10.1006/jmsc.1999.0522. PubMed PMID: WOS:000087548900029.

36. Baranova T, Müller-Karulis B, Šics I, Plikshs M. Changes in the annual life cycle of eastern Baltic cod during 1950–2010. ICES CM. 2011;10:22.
37. Ljung GM, Box GE. On a measure of lack of fit in time series models. Biometrika. 1978;65(2):297-303.
38. Durbin J, Watson GS. Testing for serial correlation in least squares regression. III. Biometrika. 1971;58(1):1-19.
39. Vallin L, Nissling A. Maternal effects on egg size and egg buoyancy of Baltic cod, Gadus morhua - Implications for stock structure effects on recruitment. Fisheries Research. 2000;49(1):21-37. doi: 10.1016/s0165-7836(00)00194-6. PubMed PMID: WOS:000165113600002.
40. Hinrichsen HH, von Dewitz B, Dierking J, Haslob H, Makarchouk A, Petereit C, et al. Oxygen depletion in coastal seas and the effective spawning stock biomass of an exploited fish species. Royal Society Open Science. 2016;3(1). doi: 10.1098/rsos.150338. PubMed PMID: WOS:000377968600005.
41. Elken J, Lehmann A, Myrberg K. Recent change—marine circulation and stratification. Second Assessment of Climate Change for the Baltic Sea Basin: Springer; 2015. p. 131-44.
42. Hixon MA, Johnson DW, Sogard SM. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science. 2013;71(8):2171-85.
43. Wasmund N, Andrushaitis A, Łysiak-Pastuszak E, Müller-Karulis B, Nausch G, Neumann T, et al. Trophic status of the south-eastern Baltic Sea: a comparison of coastal and open areas. Estuarine, Coastal and Shelf Science. 2001;53(6):849-64.
44. Gustafsson EO, Omstedt A. Sensitivity of Baltic Sea deep water salinity and oxygen concentration to variations in physical forcing. Boreal Environment Research. 2009;14(1):18-30. PubMed PMID: WOS:000264429500003.
45. Fennel W, Neumann T. Coupling biology and oceanography in models. AMBIO: A Journal of the Human Environment. 2001;30(4):232-6.
46. Wan Z, She J, Maar M, Jonasson L, Baasch-Larsen J. Assessment of a physical-biogeochemical coupled model system for operational service in the Baltic Sea. Ocean Science. 2012;8(4):683.
47. ICES Advice on fishing opportunities, catch, and effort Baltic Sea Ecoregion. ICES Advice 2016, Book 8, section 1.2.3
48. Hinrichsen H-H, Large S, Möllmann C, Müller-Karulis B, Neuenfeldt S, Norrström N, et al. Report of the Workshop on DEveloping Integrated AdviCE for Baltic Sea ecosystem-based fisheries management (WKDEICE): 18-21 April 2016 Helsinki, Finland. International Council for the Exploration of the Sea (ICES); 2016.
49. Voss R, Quaas MF, Stoeven MT, Schmidt JO, Tomczak MT, Möllmann C. Ecological-Economic Fisheries Management Advice—Quantification of Potential Benefits for the Case of the Eastern Baltic COD Fishery. Frontiers in Marine Science. 2017;4:209.

Synthesis

Summary of the results relating to the 4 main hypotheses

(1) The BDRL approach can be used as a basis for an alternative environmental recruitment indicator, which is performing better than the current use of the Spawning Stock Biomass (SSB)

According to my results presented in Chapter 1, the hypothesis (1) was confirmed. The effective Spawning Stock Biomass (eSSB), which incorporated the BDRL approach, increased the explained variation of a Ricker-Type recruitment model compared to the currently used SSB without environmental considerations (r^2(SSB) = 0.28, r^2(eSSB)= 0.39). This implies that the methodology of BDRLs improves biological forecasts, which underlines that the size-structure of the stock is relevant for the overall recruitment success, due to the differences in oxygen dependent survival of eggs at distinct neutral buoyancy depths.

(2) Drift patterns influence the use of the limited available nursery grounds for juvenile cod and the settling success of individuals depends on the spawning site

Based on the results presented in Chapter 2 the hypothesis (2) was also confirmed. The Bornholm Basin has the potential to contribute on average 57% to the total production of successfully settled juveniles, which strongly exceeds the contribution of other sub-basins, e.g. 22% from the second largest contributor, the Gdansk Deep. Furthermore, the availability and occupation of nursery habitat as well as the condition of demersal 1(year)-group cod (Fulton's K) were found to decrease in a similar rate from 1971 to 2010. This suggests that drift patterns not only severely impact the successful settlement of cod, but combined with the oxygen depending habitat they could even affect density dependent processes relevant for recruitment success.

(3) The Eastern Baltic cod spawning habitat is impacted by eutrophication and the BDRL approach performs better than the "classical" RV approach in testing such environmental impacts and dynamics of the spawning habitat

The results presented in chapter 3 indicate that the hypothesis (3) was confirmed. The BDRL as well as the RV approach identified a significant negative impact of eutrophication on the size of the spawning habitat. However, the comparison between the approaches showed that the BDRL is more sensitive to environmental change, able to incorporate stock structure, does not overestimate the spawning habitat in the Gdansk Deep and Gotland Basin and can thus be used for further applications, e.g. estimating ocean acidification levels experienced by eggs or the development of other environmental indicators.

(4) The BDRL approach can be combined with existing infrastructure, i.e. the measurement platform in the Arkona Basin equipped with salinity sensors, to perform short term forecasts of the environmental spawning conditions for Eastern

Baltic cod and the resulting indicator is suitable to inform advisory institutions of fisheries management

Due to the results presented in Chapter 4 the hypothesis (4) was also confirmed. A strong positive correlation was found between the oxygen dependent survival of eggs spawned by medium- and small-sized females in the Bornholm Basin and the salinity at the site of the existing measurement platform in the Arkona Basin. The resulting correlations were performing well in cross-validation tests, indicating that they have good forecasting abilities. Therefore, they could be applied each year in April to inform stock assessment on the likely egg survival during the following spawning season improving recruitment estimates.

Discussion and future directions

A large share of fish stocks caught for commercial reasons worldwide is overexploited (Watson and Pauly, 2001). However, both critical data on the demography of stocks as well as managing institutions equipped to apply sustainable and effective measures are often not existing (Ricard et al., 2011). For example, the management of many Mediterranean Sea fish stocks is facing short data sets not covering the entire sea and not cooperating governmental institutions (formerly-) outside the EU (Fauzai et al., 2012). For the Baltic Sea, the EU is in an extraordinary good position, because sufficient data are available and powerful institutions are in place to regulate fishing activities (EC Regulation, 2013). However, the good frame conditions are not used for a viable ecological and economical gain (Froese et al., 2018), for which the Eastern Baltic cod fishery is a good example. The scientific advice on Total Allowable Catches (TAC) for the stock was rarely followed by the EU commission (Voss et al., 2016). Scientific advice for fisheries management is constantly recommending a strong reduction of fishing effort (ICES 2016; 2017) and several times advised for a total fishing ban, but these warnings were largely ignored. Short term economic benefits and a powerful fishing industry blocked any significant catch reduction. To this end, managing the stock sustainably is rather complex considering the high economic interest, political agendas, and also scientific gaps in the understanding of crucial parts of the annual assessments (e.g. ageing of individuals; Hüssy et al., 2016).

Furthermore, my thesis is an example case that shows how in addition to fishing (ICES, 2017) abiotic factors are also important drivers of stock size (Eero et al., 2015; chapter 1). The massive increase of hypoxic areas combined with high fishing pressure brought the stock close to a collapse in 1990 (Eero et al., 2007). In recent years, the recruitment success improved (Eero et al., 2012) and the environmental conditions were varying strongly due to several MBIs (Mohrholz et al., 2015; Naumann et al., 2016), but long term improvements of the environmental conditions for Eastern Baltic cod could not be observed and the stock remained at low abundances (Köster et al., 2016; ICES, 2017). The relatively low proportion of large females in the stock, the overall poor condition of individuals (Eero et al., 2015), a system regime shift to a different stable state (Möllmann et al., 2009), as well as a constantly high fishing pressure (ICES, 2017) were all proposed as possible explanations for the lack of a positive demographic trend. The most reasonable

explanation, however, is a combination of all the above, because the abiotic habitat characteristics did not substantially improve (Köster et al., 2016) and high fishing pressure prevents any suitable condition time windows for successful recruitment to result in a significant stock size increase. Therefore, recent scientific work focuses on developing concepts and recommendations to collect and combine data sources and ultimately form fixed sets of validated indicators, incorporating all relevant levels of the ecosystem - from food web over functional diversity to long- and short-term anthropogenic impacts (Margonski et al., 2018). These indicators should be used in combination with monitoring data to assess the state of the ecosystem and set baselines for management strategies. However, the integration of new indicators into management recommendations and evaluations is developing slowly due to an insufficient use of process understanding and knowledge base. My thesis sets out to improve the tools available to management by new indicator development with the aim to increase our process understanding on how drivers impact spatio-temporal spawning habitat dynamics.

My thesis adds to the growing body of evidence that high abundances of large females could be acting as a buffer against stock decline, due to the disproportional increase in fecundity with size (Hixon et al., 2014; Mion et al., 2018; Barneche et al., 2018). Therefore, the importance of large individuals for a healthy fish stock is widely recognized (e.g. Birkeland and Dayton, 2005) and has been even acknowledged by the EU Marine Strategy Framework Directive (MSFD; EU-COM, 2008); incorporated into the descriptor 3 of the Good Environmental Status (GES): "Populations of exploited fish [..] are within safe biological limits [..] , exhibiting a [..] size distribution that is indicative of a healthy stock". My thesis underscores the importance of large individuals for the case of Eastern Baltic cod stock. It shows that the use of available habitat is female size dependent (chapter 1), i.e. the spawning habitat used by larger individuals is larger, of higher quality and less sensitive to environmental impacts (chapter 3). Fisheries management should therefore aim to improve the proportional abundance of large individuals by alleviating selectively the fishing mortality of these size classes. It would enable the stock to buffer reoccurring bad environmental conditions and over exploitation, due to the multiplying effect of higher fecundity and reproductive success of large individuals. However, the current development shows a severe decrease of the length of 50% maturity within the population (Köster et al., 2016) caused by very high fishing pressure on individuals larger than 35 cm (ICES, 2017). Effective and viable concepts to achieve the target of a healthy size distribution in the stock are still missing and thus needs to be tackled by future research and management measures.

The poor oxygen conditions within the spawning habitat (chapters 1 and 3) and juvenile nursery grounds of Eastern Baltic cod (chapter 2) during the past 20 years result from anthropogenic influences (eutrophication and climate change) and a significant decrease in the occurrence of Major Baltic Inflow events (MBI) (Mohrholz et al., 2015; chapter 3). A lower eutrophication state of the system could positively influence survival chances for spawned eggs (chapter 3). Efforts during the last 10 years to reduce the input of nutrients into the Baltic Sea (HELCOM, 2007) were partly successful, but the positive trend reversal was stagnating in recent years (Reusch et al., 2018). Taken together, due to the immense time scales for water renewal in the Baltic Sea (Meier, 2005), and as agricultural fertilizers

are stored in the soil until they are slowly released over the course of decades (Gustafsson et al., 2012), a significant reduction of the eutrophication level is not to be expected before 2070 (Gustafsson et al., 2012). Given that the ecosystem is currently in a stable state where it is dominated by the planktivorous clupeids (Möllmann e al., 2009), the high predation pressure on cod early life stages (Köster et al., 2016) is reinforcing the eutrophication induced habitat loss. The only way out is to counteract the development by a change of fishing strategies. To keep the fish stock at profitable levels, the fisheries management could apply more flexible TACs, which could react to the respective environmental conditions for recruitment. By reducing the catch substantially in years with good reproductive conditions, a large potential egg production could be secured reinforcing the year class strength and inducing a positive long-term stock development. The flexible TACs could be even combined with other proposed strategies to set alternative management targets like the "ecologically-constrained Maximum Economic Yield" (eMEY, Voss et al., 2017), which could improve the short- to long-term stability of fisheries efforts by simultaneously increasing the overall profit.

Furthermore, the importance of the Bornholm Basin as the most suitable spawning ground (chapter 1 and 3) and the spawning site with the most favourable long term drift patterns for a successful settlement of juveniles (chapter 2) could also be beneficially applied in fisheries management. The managing measure of Marine Protective Areas (MPA) is capable of implementing goals of conservation (Edgar et al., 2014), but is object to controversial debate when the increase of socio-economic benefits from fisheries is to be quantified (e.g. Di Franco et al., 2016). In the case of the Baltic Sea, MPAs are implemented mainly for conservation of highly diverse, sensitive and mostly coastal habitats, but not as fisheries management tool. In fact, only 2 of the 163 MPAs within the Baltic Sea have management plans subject to prohibit fishing activities (HELCOM, 2013). However, concluding from the results of my thesis, it could be beneficial to temporarily close fisheries for the Bornholm Basin during years with exceptionally good reproduction conditions. The closure during the entire spawning season would ensure that the high survival chances of spawned eggs (chapters 3 and 4) and the high probability for juveniles to settle successfully (chapter 2) produce a strong cohort of recruits. The effect would possibly be sufficient to strengthen the population for several years and would be relatively easy to validate using the stock size structure which is routinely assessed by the already implemented survey programs. Furthermore, it has been shown that MPAs have the potential to increase the mean size of a population (Lester et al., 2009), which could in the long term increase the impact of the proposed measure by strengthening the proportion of large individuals in the stock. However, in order to benefit from this effect, the MPA within the Bornholm Basin would have to be made more permanent than only being enforced during exceptionally good years. The stock is distributed in the entire Baltic Proper (Bartolino et al., 2017) and fishing activities are also not restricted to the Bornholm Basin (ICES, 2017), thus a MPA with a total fishing ban for the 60m isobath of the Bornholm Basin could be a feasible concept.

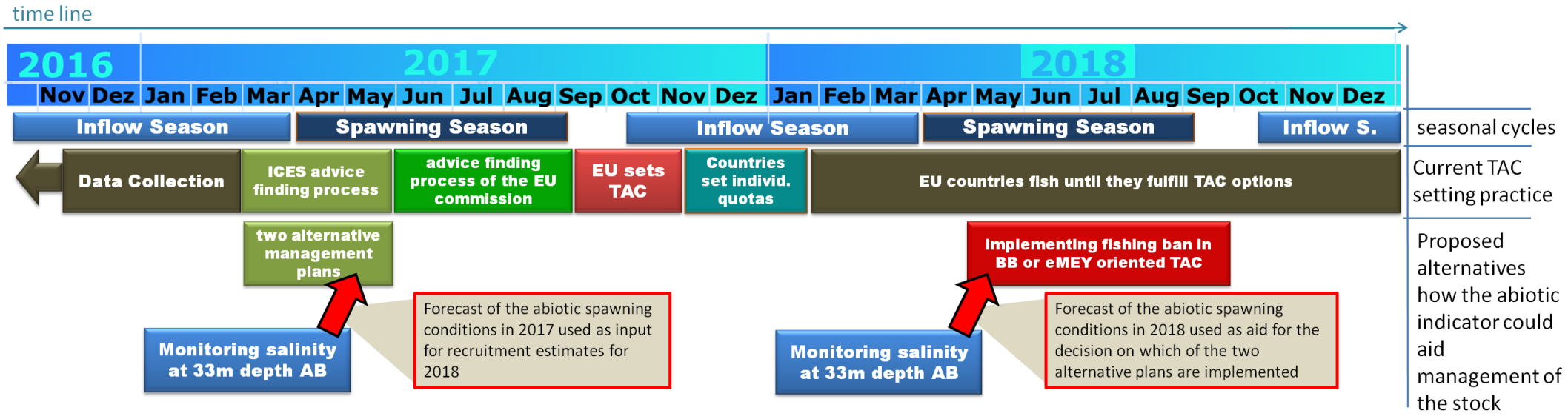

Figure 5: Schematic time line illustrating how the indicator for the abiotic spawning conditions proposed in chapter 4 could be implemented in the management of the Eastern Baltic cod stock. Shown are the seasonal reoccurrences of spawning and inflow seasons, the chronological events of the current practice to find and set TAC (Total Allowable Catch) options for each EU member state, as well as the time points at which the indicator to forecast the abiotic spawning conditions could aid sustainable management. The illustration is made with taking the example of the decision process on TAC for 2018.

The above proposed changes for the management of the Eastern Baltic cod stock require an indicator for the environmental conditions within the spawning habitat. To enable scientific advice with respect to TAC within the International Council for the Exploration of the Sea (ICES), this indicator has to fulfil the premise to forecast exceptionally good environmental conditions within the spawning habitat. Chapter 4 of my thesis is developing exactly such an indicator. The indicator is based on salinity measurements in the Arkona Basin from a permanently installed monitoring platform as a forecasting "sensor" to inform about possible MBIs. The relationship between the measured salinity in the Arkona Basin and the oxygen depending egg survival probabilities within the Bornholm Basin can then function as an early warning indicator (Fig. 5). This tool would give the ICES Baltic Fisheries Assessment Working Group (WGBFAS) and the Advisory Committee (ACOM) the chance to suggest a precautionary fishing limit to the EU, which incorporates environmental information for the coming spawning season. However, it is imperative to change the current procedures how the TAC options for Baltic cod are set in the EU in order to fully benefit from the possibilities, because the procedure from scientific advice to set EU TAC options is taking 5 to 7 months. Therefore advice on the total catch has to be given in April each year for the following year (Fig. 5). A possible solution could be to prepare two alternative strategies, which are then implemented immediately prior to the spawning season according to the newly developed indicator. If a MBI is recognised by the salinity "sensor" by April, the precautionary TAC options or a fishing ban for the Bornholm Basin would be implemented, if no inflow is recognized, an eMEY oriented TAC would be applied (Fig. 5). Another possibility could be to investigate by the use of forecasting (predicting-) models, e.g. inference- or transfer-models, and the integration of other external climate indicators, e.g. NAO, if the MBI's could be forecasted also for the following year. In combination with the newly developed indicator this would give us the opportunity to forecast the oxygen depending spawning conditions not only during the coming spawning season, but also during the spawning season the following year.

For the new indicator and other results of my thesis produced by the means of the BDRL approach, the greatest uncertainty of the newly developed methodology lies in the female size depending egg buoyancies reported by Vallin and Nissling (2000), which were used to calculate the mean egg buoyancies per females size class. The experiments were never repeated in sufficient numbers and size ranges of individuals, but prior studies on Atlantic cod found relationships of female size to eggs size (Kjesbu, 1989; Marteinsdottir and Steirnarsson, 1998) or egg size to egg density (Kjesbu et al., 1992). Petereit et al. (2014) could not identify any relationship between female size and egg buoyancy for the western Baltic cod population, but his results can only partially be transferred to my thesis, as he tested mostly first spawning individuals, i.e. small females, from the distinct western population. However, this implies that there might be a slight discrepancy of the exact water densities of neutral egg buoyancy in contrast to the assumptions of the population mean used throughout my thesis. Due to the egg buoyancy ranges found in the field (Hinrichsen et al., 2016) and the stock size structure effects on recruitment (Cardniale and Arrehnius, 2000; chapters 1 and 3), it is very unlikely that the basic relationship between female spawner size and buoyancy will be disproved by future research. And even if future studies suggest slightly changed egg densities for the females spawner size classes, they

are not likely to change the overall findings and the applicability of the methodology. However, it is crucial to increase the knowledge on this unique adaptation of the Eastern Baltic cod population to the local environmental conditions, which will allow us to further advance the presented method of BDRLs and therefore simultaneously improve the available tools for stock management.

The BDRL methodology makes use of water density levels of neutral egg buoyancy and the environmental conditions on these water density levels. Therefore, it would be also applicable to other fish species in the Baltic Sea with pelagic eggs, e.g. plaice and flounder (Petereit et al., 2014), although for these two species, the size of the female could not yet be related to the depth of neutral egg buoyancy. However, the range of egg densities occurring within these species (Petereit et al., 2014; Nissling et al., 2002; Hinrichsen et al., 2016) could already be used to map habitat sizes and characteristics in the Baltic Sea. This would ultimately lead to a better understanding of the spawning habitat quality. To investigate the relationship between female size and egg buoyancy also within these fish species, experiments with eggs from females of a large sizes range are crucially needed. The research could help to improved tools for scientific advisory institutions and ultimately stock management. A further goal would be to integrate population dynamics of all fish species together with environmental indicators for recruitment as well as biogeochemical models simulating the development of lower trophic levels to secure a reasonable management of the entire Baltic Sea ecosystem.

Concluding remarks

Since anthropogenic impacts reduce the abundance of fish species worldwide and the world population of about 11 billion people in 2100 (UN, 2015) will rely more and more on fish as a protein source, the current use of the resource has to change on a global scale. If the negative trend of global catches and the decrease of fish stocks worldwide (Costello et al., 2016; Zeller et al., 2018) is further neglected the impacts of climate change, coastal eutrophication and overfishing could lead to a collapse of the majority of stocks (Teh et al., 2017) and the demands would not be able to be fulfilled. Therefore, not only viable management strategies have to be further developed and the biological knowledge expanded, but also new concepts how international law and treaties can enforce the measures are needed. The Baltic Sea can act here as an experimental environment with many nations sharing a common good that needs to be managed together and could form the basis for pioneer work how the resource fish could be managed on a global scale. The Baltic Sea demonstrates that abiotic drivers have to be considered as integrated part of successful management plans (Reusch et al., 2018). More flexibility in setting the targeted catches and long term precautionary limits are needed in order to keep the stock size within safe biological limits. Furthermore, the conservation of habitats is crucial for a sustainable exploitation of fish stocks and further measures are needed to insure a healthy environment for healthy fish stocks. The decision about the common resource fish is currently made out of short sided reasons for fast profit, which needs to be made visible for the brought public by more transparency of the decision process. The resource is limited and the standards of

conservation should be adjusted to the standards applied to resources on land in the EU already.

My thesis gives new insight into how abiotic drivers act on one of the most overexploited Baltic fish stocks and presents how the developed novel environmental indicator could be applied in a common long-term management strategy. It furthermore emphasizes the importance of the Bornholm Basin as the main spawning location crucially needed for the recruitment of the stock. The management of other fish stocks could use similar approaches to identify and protect the key habitat for the particular stock and therefore ensure further profitable exploitation of the stock. Specifically, for the Eastern Baltic cod stock, I hope future research continues to develop and integrate the BDRL approach into stock management. The ultimate aim should be to combine the approach with other validated environmental and stock indicators, and use those as input for further developed integrated ecosystem based models. Therefore, I hope that my thesis will help to enable future generations to enjoy, exploit and conserve fish populations within the Baltic Sea and worldwide and to make people realize that these activities don’t have to be contradictory.

References

Andersen, J. H., Carstensen, J., Conley, D. J., Dromph, K., Fleming-Lehtinen, V., Gustafsson, B. G., et al. (2017). Long- term temporal and spatial trends in eutrophication status of the Baltic Sea. Biological Reviews, 92(1), 135-149.

Bagge, O., Thurow, F., Steffensen, E., Bay, J., 1994. The Baltic cod. Dana 10, 1–28.

Baranova, T., Mu¨ller-Karulis, B., _Sics, I., and Plikshs, M. (2011). Changes in the annual life cycle of Eastern Baltic Cod during 1950-2010. ICES Document CM 2011/R: 10.

Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. [10.1126/science.aao6868]. *Science, 360*(6389), 642.

Bartolino, V., Tian, H., Bergström, U., Jounela, P., Aro, E., Dieterich, C., et al. (2017). Spatio-temporal dynamics of a fish predator: Density-dependent and hydrographic effects on Baltic Sea cod population. PLOS ONE, 12(2), e0172004.

Berg, P. R., Jentoft, S., Star, B., Ring, K. H., Knutsen, H., Lien, S., et al. (2015). Adaptation to Low Salinity Promotes Genomic Divergence in Atlantic Cod (Gadus morhua L.). Genome Biology and Evolution, 7(6), 1644-1663.

Bergström, S., & Carlsson, B. (1994). RIVER RUNOFF TO THE BALTIC SEA - 1950-1990. [article]. Ambio, 23(4-5), 280-287.

Birkeland, C., & Dayton, P. K. (2005). The importance in fishery management of leaving the big ones. Trends in Ecology & Evolution, 20(7), 356-358.

Bleil, M., & Oeberst, R. (1998). The spawning of cod (Gadus morhua morhua) under controlled conditions of captivity, quantity and quality of spawned eggs. ICES CM, 1000(3).

Bleil, M., Oeberst, R., & Urrutia, P. (2009). Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. Journal of Applied Ichthyology, 25(1), 10-17.

Blenckner, T., Österblom, H., Larsson, P., Andersson, A., & Elmgren, R. (2015). Baltic Sea ecosystem-based management under climate change: Synthesis and future challenges. AMBIO, 44(3), 507-515.

Broeg, K., & Lehtonen, K. K. (2006). Indices for the assessment of environmental pollution of the Baltic Sea coasts: Integrated assessment of a multi-biomarker approach. Marine Pollution Bulletin, 53(8), 508-522.

Burchard, H., Janssen, F., Bolding, K., Umlauf, L., & Rennau, H. (2009). Model simulations of dense bottom currents in the Western Baltic Sea. [Article; Proceedings Paper]. Continental Shelf Research, 29(1), 205-220.

Cardinale, M., & Arrhenius, F. (2000). The influence of stock structure and environmental conditions on the recruitment process of Baltic cod estimated using a generalized additive model. *Canadian Journal of Fisheries and Aquatic Sciences, 57*(12), 2402-2409.

Carpenter, G. (2016). Landing the blame: Overfishing in the Baltic Sea 2016.

Carstensen, J., Andersen, J. H., Gustafsson, B. G., & Conley, D. J. (2014). Deoxygenation of the Baltic Sea during the last century. Proceedings of the National Academy of Sciences of the United States of America, 111(15), 5628-5633.

Casini, M., Blenckner, T., Mollmann, C., Gardmark, A., Lindegren, M., Llope, M., et al. (2012). Predator transitory spillover induces trophic cascades in ecological sinks. *Proceedings of the National Academy of Sciences of the United States of America, 109*(21), 8185-8189.

Casini, M., Käll, F., Hansson, M., Plikshs, M., Baranova, T., Karlsson, O., et al. (2016). Hypoxic areas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. Royal Society open science, 3(10), 160416.

Casini, M., Möllmann, C., & Österblom, H. (2011). Ecosystem approach to fisheries in the Baltic Sea: present and potential future applications in assessment and management. In "Ecosystem Based Management for Fisheries-An Evolving Perspective". A. Belgrano and C. Fowler Eds: Cambridge University Press.

Chabot, D., & Dutil, J. D. (1999). Reduced growth of Atlantic cod in non- lethal hypoxic conditions. Journal of Fish Biology, 55(3), 472-491.

Conley, D. J., Bjorck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., et al. (2009). Hypoxia-Related Processes in the Baltic Sea. Environmental Science & Technology, 43(10), 3412-3420.

Conley, D. J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., et al. (2011). Hypoxia Is Increasing in the Coastal Zone of the Baltic Sea. Environmental Science & Technology, 45(16), 6777-6783.

Conley, D. J., Humborg, C., Rahm, L., Savchuk, O. P., & Wulff, F. (2002). Hypoxia in the Baltic Sea and basin-scale changes in phosphorus biogeochemistry. Environmental Science & Technology, 36(24), 5315-5320.

Costello, C., Ovando, D., Clavelle, T., Strauss, C. K., Hilborn, R., Melnychuk, M. C., et al. (2016). Global fishery prospects under contrasting management regimes. Proceedings of the national academy of sciences, 201520420.

Di Franco, A., Thiriet, P., Di Carlo, G., Dimitriadis, C., Francour, P., Gutiérrez, N. L., et al. (2016). Five key attributes can increase marine protected areas performance for small-scale fisheries management. [Article]. Scientific Reports, 6, 38135.

Diaz, R. J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. science, 321(5891), 926-929.

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., et al. (2014). Global conservation outcomes depend on marine protected areas with five key features. Nature, 506, 216.

Eero, M., Hjelm, J., Behrens, J., Buchmann, K., Cardinale, M., Casini, M., et al. (2015). Eastern Baltic cod in distress: biological changes and challenges for stock assessment. ICES Journal of Marine Science, 72(8), 2180-2186.

Eero, M., Koster, F. W., Plikshs, M., & Thurow, F. (2007). Eastern Baltic cod (Gadus morhua callarias) stock dynamics: extending the analytical assessment back to the mid-1940s. Ices Journal of Marine Science, 64(6), 1257-1271.

Eero, M., Köster, F. W., & Vinther, M. (2012). Why is the Eastern Baltic cod recovering? Marine Policy, 36(1), 235-240.

Eilola, K. (1997). Development of a spring thermocline at temperatures below the temperature of maximum density with application to the Baltic Sea. *Journal of Geophysical Research: Oceans*, *102*(C4), 8657-8662.

Elken, J., & Matthäus, W. (2008). Baltic Sea oceanography.

EU-COM (2008) Directive 2008/56/EC of the European parliament and of the council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive).

Falk-Petersen, I. B. (2005). Comparative organ differentiation during early life stages of marine fish. Fish & Shellfish Immunology, 19(5), 397-412.

Fennel, W., Seifert, T., & Kayser, B. (1991). Rossby radii and phase speeds in the Baltic Sea. Continental Shelf Research, 11(1), 23-36.

Fouzai, N., Coll, M., Palomera, I., Santojanni, A., Arneri, E., & Christensen, V. (2012). Fishing management scenarios to rebuild exploited resources and ecosystems of the Northern-Central Adriatic (Mediterranean Sea). Journal of Marine Systems, 102-104, 39-51.

Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A. C., Dimarchopoulou, D., et al. (2018). Status and rebuilding of European fisheries. Marine Policy, 93, 159-170.

Fulton, E. A. (2010). Approaches to end-to-end ecosystem models. Journal of Marine Systems, 81(1), 171-183.

Grauman, G. B. (1973). Investigations of factors influencing fluctuations in abundance of Baltic cod. Rap. Proces, 146, 73-76.

Grønkjær, P., & Wieland, K. (1997). Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Marine Ecology Progress Series, 91-105.

Gustafsson, B. G., Schenk, F., Blenckner, T., Eilola, K., Meier, H. E. M., Muller-Karulis, B., et al. (2012). Reconstructing the Development of Baltic Sea Eutrophication 1850-2006. [Article]. Ambio, 41(6), 534-548.

Harvey, C. J., Cox, S. P., Essington, T. E., Hansson, S., & Kitchell, J. F. (2003). An ecosystem model of food web and fisheries interactions in the Baltic Sea. ICES Journal of Marine Science, 60(5), 939-950.

HELCOM (2007). Climate Change in the Baltic Sea Area – HELCOM Thematic Assessment in 2007. Baltic Sea Environment Proceedings No. 111.

HELCOM (2013). HELCOM PROTECT- Overview of the status of the network of Baltic Sea marine protected areas. 31 pp.

Herlemann, D. P. R., Labrenz, M., Jürgens, K., Bertilsson, S., Waniek, J. J., & Andersson, A. F. (2011). Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. [Original Article]. The Isme Journal, 5, 1571.

Hinrichsen, H. H., Huwer, B., Makarchouk, A., Petereit, C., Schaber, M., & Voss, R. (2011). Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (Gadus morhua). Ices Journal of Marine Science, 68(10), 2019-2028.

Hinrichsen, H. H., Kuhn, W., Peck, M. A., & Voss, R. (2012). The impact of physical and biological factors on the drift and spatial distribution of larval sprat: A comparison of the Baltic and North Seas. Progress in Oceanography, 107, 47-60.

Hinrichsen, H. H., von Dewitz, B., Dierking, J., Haslob, H., Makarchouk, A., Petereit, C., et al. (2016). Oxygen depletion in coastal seas and the effective spawning stock biomass of an exploited fish species. *Royal Society Open Science, 3*(1).

Hinrichsen, H. H., Lehmann, A., Möllmann, C., & Schmidt, J. O. (2003). Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. Fisheries Oceanography, 12(4- 5), 425-433.

Hinrichsen, H. H., Mollmann, C., Voss, R., Koster, F. W., & Kornilovs, G. (2002). Biophysical modeling of larval Baltic cod (Gadus morhua) growth and survival. Canadian Journal of Fisheries and Aquatic Sciences, 59(12), 1858-1873.

Huwer, B., Clemmesen, C., Gronkjaer, P., & Koster, F. W. (2011). Vertical distribution and growth performance of Baltic cod larvae - Field evidence for starvation-induced recruitment regulation during the larval stage? Progress in Oceanography, 91(4), 382-396.

Huwer, B., Neuenfeldt, S., Rindorf, A., Andreasen, H., Levinsky, S.-E., Storr-Paulsen, M., et al. (2014). Study on stomach content of fish to support the assessment of good environmental status of marine food webs and the prediction of MSY after stock restoration: European Commission.

Hüssy, K., Mosegaard, H., Hinrichsen, H. H., & Böttcher, U. (2003). Using otolith microstructure to analyse growth of juvenile Baltic cod Gadus morhua. Marine Ecology Progress Series, 258, 233-241.

Hüssy, K., Radtke, K., Plikshs, M., Oeberst, R., Baranova, T., Krumme, U., et al. (2016). Challenging ICES age estimation protocols: lessons learned from the eastern Baltic cod stock. ICES Journal of Marine Science, 73(9), 2138-2149.

Hüssy, K., St. John, M. A., & Böttcher, U. (1997). Food resource utilization by juvenile Baltic cod Gadus morhua: a mechanism potentially influencing recruitment success at the demersal juvenile stage? Marine Ecology Progress Series, 199-208.

(ICES) Karpushevskaia, A., Nielsen, A., Mikhaylov, A., Luzenczyk, A., Florin, A.-B., Albert, A., et al. (2016). Report of the Baltic Fisheries Assessment Working Group (WGBFAS), 12-19 April 2016, ICES HQ, Copenhagen, Denmark: International Council for the Exploration of the Sea.

(ICES) Orio, A., Nielsen, A., Luzenczyk, A., Berg, C., Ustups, D., Artemenkov, D., et al. (2017). Report of the Baltic Fisheries AssessmentWorking Group (WGBFAS): 19-26 April 2017, Copenhagen, Denmark: International Council for the Exploration of the Sea.

Kjesbu, O. S. (1989). THE SPAWNING ACTIVITY OF COD, GADUS-MORHUA L. Journal of Fish Biology, 34(2), 195-206.

Kjesbu, O.S., Kryvi, H., Sundby, S., Solemdal, P., (1992). Buoyancy variations in eggs of Atlantic cod (Gadus morhua L.) in relation to chorion thickness and egg size: theory and observations. Journal of Fish Biology 41, 581–599.

Kotta, J., Nurkse, K., Puntila, R., & Ojaveer, H. (2016). Shipping and natural environmental conditions determine the distribution of the invasive non-indigenous

round goby Neogobius melanostomus in a regional sea. Estuarine, Coastal and Shelf Science, 169, 15-24.

Krauss, W., & Brugge, B. (1991). WIND-PRODUCED WATER EXCHANGE BETWEEN THE DEEP BASINS OF THE BALTIC SEA. Journal of Physical Oceanography, 21(3), 373-384.

Köster, F., Vinther, M., MacKenzie, B., Eero, M., & Plikshs, M. (2009). Environmental effects on recruitment and implications for biological reference points of Eastern Baltic cod (Gadus morhua). [Journal article]. *Journal of Northwest Atlantic Fishery Science, 41*, 205-220.

Köster, F. W., Hinrichsen, H.-H., St. John, M. A., Schnack, D., MacKenzie, B. R., Tomkiewicz, J., et al. (2001). Developing Baltic cod recruitment models. II. Incorporation of environmental variability and species interaction. Canadian Journal of Fisheries and Aquatic Sciences, 58(8), 1534-1556.

Köster, F. W., Mollmann, C., Hinrichsen, H.-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., et al. (2005). Baltic cod recruitment - the impact of climate variability on key processes. Ices Journal of Marine Science 62:1408-1425.

Köster, F. W., Huwer, B., Hinrichsen, H.-H., Neumann, V., Makarchouk, A., Eero, M., et al. (2016). Eastern Baltic cod recruitment revisited—dynamics and impacting factors. ICES Journal of Marine Science, 74(1), 3-19.

Lehmann, A. (1995). A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. Tellus A, 47(5), 1013-1031.

Lehmann, A., & Hinrichsen, H. H. (2000). On the thermohaline variability of the Baltic Sea. Journal of Marine Systems, 25(3-4), 333-357.

Lehmann, A., Hinrichsen, H. H., Getzlaff, K., & Myrberg, K. (2014). Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach. Journal of Marine Systems, 134, 20-28.

Lehmann, A., Krauss, W., & Hinrichsen, H. H. (2002). Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus Series a-Dynamic Meteorology and Oceanography, 54(3), 299-316.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., et al. (2009). Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series, 384, 33-46.

Lindegren, M., Möllmann, C., Nielsen, A., Brander, K., MacKenzie, B. R., & Stenseth, N. C. (2010). Ecological forecasting under climate change: the case of Baltic cod. Proceedings of the Royal Society of London B: Biological Sciences, rspb20100353.

MacKenzie, B., John, M. S., & Wieland, K. (1996). Eastern Baltic cod: Perspectives from existing data on processes affecting growth and survival of eggs and larvae. [Review]. *Marine Ecology-Progress Series, 134*(1-3), 265-281.

MacKenzie, B. R., Hinrichsen, H. H., Plikshs, M., Wieland, K., & Zezera, A. S. (2000). Quantifying environmental heterogeneity: habitat size necessary for successful development of cod Gadus morhua eggs in the Baltic Sea. [Article]. Marine Ecology-Progress Series, 193, 143-156.

Margonski, P., Andersson, H., von Dewitz, B., Eero, M., Hinrichsen, H.-H., Jonsson, P., et al. (2018). Report on evaluation framework for holistic management ? summary of the concept, requirements and management implications: EU Bonusproject BIO-C3.

Marteinsdóttir, G., & Steinarsson, A. (1998). Maternal influence on the size and viability of Iceland cod Gadus morhua eggs and larvae. Journal of Fish Biology, 52(6), 1241-1258.

Matthäus, W., & Franck, H. (1992). Characteristics of major Baltic inflows—a statistical analysis. Continental Shelf Research, 12(12), 1375-1400.

Meier, H. E. M. (2005). Modeling the age of Baltic Seawater masses: Quantification and steady state sensitivity experiments. Journal of Geophysical Research: Oceans, 110(C2).

Melzner, F., Thomsen, J., Koeve, W., Oschlies, A., Gutowska, M., Bange, H., et al. (2012). Future ocean acidification will be amplified by hypoxia in coastal habitats. Marine Biology, 1-14.

Mion, M. , Thorsen, A. , Vitale, F. , Dierking, J. , Herrmann, J. P., Huwer, B. , von Dewitz, B. and Casini, M. (2018), Effect of fish length and nutritional condition on the fecundity of distressed Atlantic cod *Gadus morhua* from the Baltic Sea. J Fish Biol, 92: 1016-1034.

Mohrholz, V., Naumann, M., Nausch, G., Krüger, S., & Gräwe, U. (2015). Fresh oxygen for the Baltic Sea—An exceptional saline inflow after a decade of stagnation. Journal of Marine Systems, 148, 152-166.

Möllmann, C., Blenckner, T., Casini, M., Gardmark, A., & Lindegren, M. (2011). Beauty is in the eye of the beholder: management of Baltic cod stock requires an ecosystem approach. Marine Ecology Progress Series, 431, 293-297.

Möllmann, C., Diekmann, R., Muller-Karulis, B., Kornilovs, G., Plikshs, M., & Axe, P. (2009). Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. Global Change Biology, 15(6), 1377-1393.

Möllmann, C., Lindegren, M., Blenckner, T., Bergström, L., Casini, M., Diekmann, R., et al. (2013). Implementing ecosystem-based fisheries management: from single-species to integrated ecosystem assessment and advice for Baltic Sea fish stocks. ICES Journal of Marine Science, 71(5), 1187-1197.

Möllmann, C., Müller-Karulis, B., Kornilovs, G., & St John, M. A. (2008). Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. ICES Journal of Marine Science, 65(3), 302-310.

United Nations. (2015). World population prospects: The 2015 revision. United Nations Econ Soc Aff, 33(2), 1-66.

Naumann, M., Nausch, G., & Mohrholz, V. (2016). A succession of four Major Baltic Inflows in the period 2014-2016–an overview of propagation and environmental change. Multiple drivers for Earth system changes in the Baltic Sea region, 27.

Nieminen, E., Lindroos, M., & Heikinheimo, O. (2012). Optimal Bioeconomic Multispecies Fisheries Management: A Baltic Sea Case Study. Marine Resource Economics, 27(2), 115-136.

Nissling, A., & Vallin, L. (1996). The ability of Baltic cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. Journal of Fish Biology, 48(2), 217-227.

Nissling, A., & Westin, L. (1991). Egg buoyancy of Baltic cod (Gadus morhua) and its implications for cod stock fluctuations in the Baltic. Marine Biology, 111(1), 33-35.

Nissling, A., & Westin, L. (1997). Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. [Article]. Marine Ecology-Progress Series, 152(1-3), 261-271.

Nissling, A., Westin, L., & Hjerne, O. (2002). Reproductive success in relation to salinity for three flatfish species, dab (Limanda limanda), plaice (Pleuronectes platessa), and flounder (Pleuronectes flesus), in the brackish water Baltic Sea. Ices Journal of Marine Science, 59(1), 93-108.

Ojaveer, H., Jaanus, A., MacKenzie, B. R., Martin, G., Olenin, S., Radziejewska, T., et al. (2010). Status of Biodiversity in the Baltic Sea. Plos One, 5(9).

Ojaveer, H., Olenin, S., Narščius, A., Florin, A.-B., Ezhova, E., Gollasch, S., et al. (2017). Dynamics of biological invasions and pathways over time: a case study of a temperate coastal sea. Biological Invasions, 19(3), 799-813.

Omstedt, A., Elken, J., Lehmann, A., & Piechura, J. (2004). Knowledge of the Baltic Sea physics gained during the BALTEX and related programmes. Progress in Oceanography, 63(1-2), 1-28.

Oschlies, A. (2009). Simulated 21(st) century's increase in oceanic suboxia by CO2-enhanced biotic carbon export. Geochimica Et Cosmochimica Acta, 73(13), A977-A977.

Pecuchet, L., Nielsen, J. R., & Christensen, A. (2014). Impacts of the local environment on recruitment: A comparative study of North Sea and Baltic Sea fish stocks (Vol. 72).

Petereit, C., Hinrichsen, H. H., Franke, A., & Köster, F. W. (2014). Floating along buoyancy levels: Dispersal and survival of western Baltic fish eggs. Progress in Oceanography, 122, 131-152.

Plikshs, M., Hinrichsen, H. H., Elferts, D., Sics, I., Kornilovs, G., & Köster, F. W. (2015). Reproduction of Baltic cod, Gadus morhua (Actinopterygii: Gadiformes: Gadidae), In the Gotland Basin: Causes of annual variability. *Acta Ichthyologica Et Piscatoria, 45*(3), 247-258.

Plikshs, M., Kalejs, M., & Grauman, G. (1993). The Influence of Environmental Conditions and Spawning Stock Size on the Year Class Strength of the Eastern Baltic cod (Vol. 22).

Pinnegar, J.K., Cheung, W.W.L., Jones, M., Merino, G., Turrell, B. and Reid, D. (2013) Impacts of climate change on fisheries. *MCCIP Science Review 2013,* 302-317.

Radtke, H., Lipka, M., Bunke, D., Morys, C., Cahill, B., Böttcher, M. E., et al. (2018). Ecological ReGional Ocean Model with vertically resolved sediments (ERGOM SED 1.0): Coupling benthic and pelagic biogeochemistry of the south-western Baltic Sea. *Geosci. Model Dev. Discuss., 2018*, 1-42.

Rak, D., & Wieczorek, P. (2012). Variability of temperature and salinity over the last decade in selected regions of the southern Baltic Sea. Oceanologia, 54(3), 339-354.

Regulation, E. C. (2013). No. 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC. Official Journal of the European Union. L, 354, 22-61.

Reissmann, J. H., Burchard, H., Feistel, R., Hagen, E., Lass, H. U., Mohrholz, V., et al. (2009). Vertical mixing in the Baltic Sea and consequences for eutrophication - A review. [Review]. Progress in Oceanography, 82(1), 47-80.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., et al. (2018). The Baltic Sea as a time machine for the future coastal ocean. [10.1126/sciadv.aar8195]. Science Advances, 4(5).

Ricard, D., Minto, C., Jensen Olaf, P., & Baum Julia, K. (2011). Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. Fish and Fisheries, 13(4), 380-398.

Rohlf, N. 1999. Aktivität und Vertikalwanderung der Larven des Ostseedorsches (Gadus morhua callarias) während der Dottersackphase. PhD thesis, Institute of Marine Sciences, Kiel. Berichte Institut für Meereskunde Kiel, Nr. 312. 60 pp.

Schinke, H., & Matthäus, W. (1998). On the causes of major Baltic inflows —an analysis of long time series. Continental Shelf Research, 18(1), 67-97.

Stigebrandt, A. (1987a). A MODEL FOR THE VERTICAL CIRCULATION OF THE BALTIC DEEP-WATER. Journal of Physical Oceanography, 17(10), 1772-1785.

Stigebrandt, A. (1987b). Computations of the flow of dense water into the Baltic Sea from hydrographical measurements in the Arkona Basin. Tellus A, 39(2), 170-177.

Stramma, L., Schmidtko, S., Levin, L. A., & Johnson, G. C. (2010). Ocean oxygen minima expansions and their biological impacts. *Deep-Sea Research Part I-Oceanographic Research Papers, 57*(4), 587-595.

Tedesco, L., Piroddi, C., Kämäri, M., & Lynam, C. (2016). Capabilities of Baltic Sea models to assess environmental status for marine biodiversity. Marine Policy, 70, 1-12.

Teh, L. S. L., Cheung, W. W. L., Christensen, V., & Sumaila, U. R. (2017). Can we meet the Target? Status and future trends for fisheries sustainability. Current Opinion in Environmental Sustainability, 29, 118-130.

Tomkiewicz, J., & Köster, F. W. (1999). Maturation processes and spawning time of cod in the Bornholm Basin of the Baltic Sea: preliminary results. ICES CM, 25.

Uzars, D., & Plikshs, M. (2000). Cod (Gadus morhua L.) cannibalism in the Central Baltic: interannual variability and influence of recruit abundance and distribution. ICES Journal of Marine Science, 57(2), 324-329.

Vainikka, A., Gårdmark, A., Bland, B., & Hjelm, J. (2009). Two- and three-dimensional maturation reaction norms for the eastern Baltic cod, Gadus morhua. ICES Journal of Marine Science, 66(2), 248-257.

Vallin, L., & Nissling, A. (2000). Maternal effects on egg size and egg buoyancy of Baltic cod, Gadus morhua - Implications for stock structure effects on recruitment. Fisheries Research, 49(1), 21-37.

von Dewitz, B., Tamm, S., Höflich, K., Voss, R., & Hinrichsen, H.-H. (2018). Use of existing hydrographic infrastructure to forecast the environmental spawning conditions for Eastern Baltic cod. PLOS ONE, 13(5), e0196477.

von Westernhagen, H., 1970. Erbrüten der Eier von Dorsch (Gadus morhua), Flunder (Pleuronectes flesus) and Scholle (Pleuronectes platessa) unter kombinierten Temperatur- und Salzgehaltsbedingungen. Helgoländer Wissenschaftliche Meeresuntersuchungen, 21: 21–102.

Voss, R., Hoffmann, J., Llope, M., Schmidt, J. O., Möllmann, C., & Quaas, M. F. (2016). Political overfishing: Social-economic drivers in TAC setting decisions: Kiel University Working Paper. Available online at: https://www. eree. uni-kiel. de/de/Political% 20overfishing% 2011% 20Sep_Julia. pdf.

Voss, R., Köster, F. W., & Dickmann, M. (2003). Comparing the feeding habits of co-occurring sprat (Sprattus sprattus) and cod (Gadus morhua) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research, 63(1), 97-111.

Voss, R., Quaas, M. F., Stoeven, M. T., Schmidt, J. O., Tomczak, M. T., & Möllmann, C. (2017). Ecological-Economic Fisheries Management Advice—Quantification of Potential Benefits for the Case of the Eastern Baltic COD Fishery. Frontiers in Marine Science, 4, 209.

Watson, R., & Pauly, D. (2001). Systematic distortions in world fisheries catch trends. Nature, 414, 534.

Wieland, K. (1995). Einfluß der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (Gadus morhua callarias) im Bornholmbecken, südliche zentrale Ostsee.

Wieland, K., Jarre-Teichmann, A., & Horbowa, K. (2000). Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. *Ices Journal of Marine Science, 57*(2), 452-464.

Zeller, D., Cashion, T., Palomares, M., & Pauly, D. (2018). Global marine fisheries discards: a synthesis of reconstructed data. Fish and Fisheries, 19(1), 30-39.

Zettler, M. L., Karlsson, A., Kontula, T., Gruszka, P., Laine, A. O., Herkül, K., et al. (2014). Biodiversity gradient in the Baltic Sea: a comprehensive inventory of macrozoobenthos data. Helgoland Marine Research, 68(1), 49-57.

Zillén, L., Conley, D. J., Andrén, T., Andrén, E., & Björck, S. (2008). Past occurrences of hypoxia in the Baltic Sea and the role of climate variability, environmental change and human impact. Earth-Science Reviews, 91(1), 77-92.

Eidesstattliche Erklärung

Hiermit erkläre ich, Burkhard von Dewitz, dass ich die vorliegende Dissertation mit dem Titel:

Drivers dynamics and management of Eastern Baltic cod (Gadus morhua) reproduction habitat

selbständig, mit der Beratung meiner Betreuer, verfasst habe. Die Dissertation ist in Form und Inhalt meine eigene Arbeit und es wurden keine anderen als die angegebenen Hilfsmittel und Quellen verwendet. Die Arbeit ist unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft entstanden.

Diese Arbeit wurde an keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt und ist mein erstes und einziges Promotionsverfahren.

Zur Veröffentlichung eingereichte Manuskripte sind jeweils am Anfang der Kapitel und im Abschnitt "Author contributions" kenntlichgemacht.

Ich erkläre mich hiermit damit einverstanden, dass diese Arbeit an die Bibliothek des GEOMARs Helmholtz Zentrum für Ozeanforschung Kiel und der Christian-Albrechts-Universität zu Kiel weitergeleitet wird.

Kiel, den 09.08.2018

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Burkhard von Dewitz

Author contributions

Chapter 1

Oxygen depletion in coastal seas and the effective spawning stock biomass of an exploited fish species

Authors: Hans-Harald Hinrichsen, Burkhard von Dewitz, Jan Dierking, Holger Haßlob, Andrej Makarchouk, Christoph Petereit, Rüdiger Voss

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H.H.H. designed the study in collaboration with B.v.D. and J.D. The stock-recruitment model related work was performed by R.V.. A.M., B.v.D., J.D., H.H. and C.P. provided the necessary biological process information and H.H.H. provided the physical data for this study. The first manuscript was drafted by H.H.H. and significantly improved by all other authors.

Chapter 2

Spatio-temporal dynamics of cod nursery areas in the Baltic Sea

Authors: Hans-Harald Hinrichsen, Burkhard von Dewitz, Andreas Lehmann, Ulf Bergström, Karin Hüssy

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H.H.H. designed the study in collaboration with B.v.D. Sea going activities and analyses of biological field samples were performed by K.H. and H.H.H.. B.v:D. U.B and K.H. also provided the necessary biological parameters and process information and H.H.H. and B.v.D. provided the physical data and conducted the biophysical model runs for this study. All authors were involved in the analyses and the interpretation of the field data and modeling results as well as in manuscript writing. Figures were prepared by B.vD. H.H.H. and K.H.

Chapter 3

Hindcasting the sensitivity to eutrophication of the Eastern Baltic cod (*Gadhus morhua*) spawning habitat

Authors: Burkhrad von Dewitz, Hans-Harald Hinrichsen, Joachim Gröger, Klaus Getzlaf, Thorsten Reusch

Will be submitted to PLoS ONE

B.v.D. and H.H.H. designed the study in collaboration with T.R.. K.G., B.v.D. and H.H.H. provided input data and K.G. supervised oceanic modelling. Statistical analysis were performed by B.v.D. with support from J.G.. The first version of the manuscript including all figures was drafted by B.v.D. and significantly improved by H.H.H., J.G. and T.R..

Chapter 4

Use of existing hydrographic infrastructure to forecast the environmental spawning conditions for Eastern Baltic cod

Authors: Burkhard von Dewitz, Susanne Tamm, Katharina Höflich, Rüdiger Voss, Hans-Harald Hinrichsen

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B.v.D. and H.H.H. designed the study. S.T., H.H.H., K.H. and B.v.D. provided input data. Methodology and statistical analysis were developed and performed by B.vD. with support from H.H.H., K.H. and R.V.. Figures were designed by B.v.D. with support from K.H. and S.T.. The first version of the manuscript was drafted by B.v.D. and significantly improved by all co-authors. The editing during revisions was performed by B.v.D. in collaboration with all co-authors.

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